

Cours d'Été O.T.A.N.

N.A.T.O. Advanced Study Institute



LES SYSTÈMES SONARS ANIMAUX

Biologie et Bionique

ANIMAL SONAR SYSTEMS



Biology and Bionics

Tome II

Frascati, Italie

26 sept. - 3 oct. 1966



Édité par René-Guy BUSNEL

LABORATOIRE DE PHYSIOLOGIE ACOUSTIQUE

INRA - CNRZ - Jouy-en-Josas - 78

France

Avec l'aide financière de l'O.N.R., de l'U.S.A.F. et de l'E.O.A.R.



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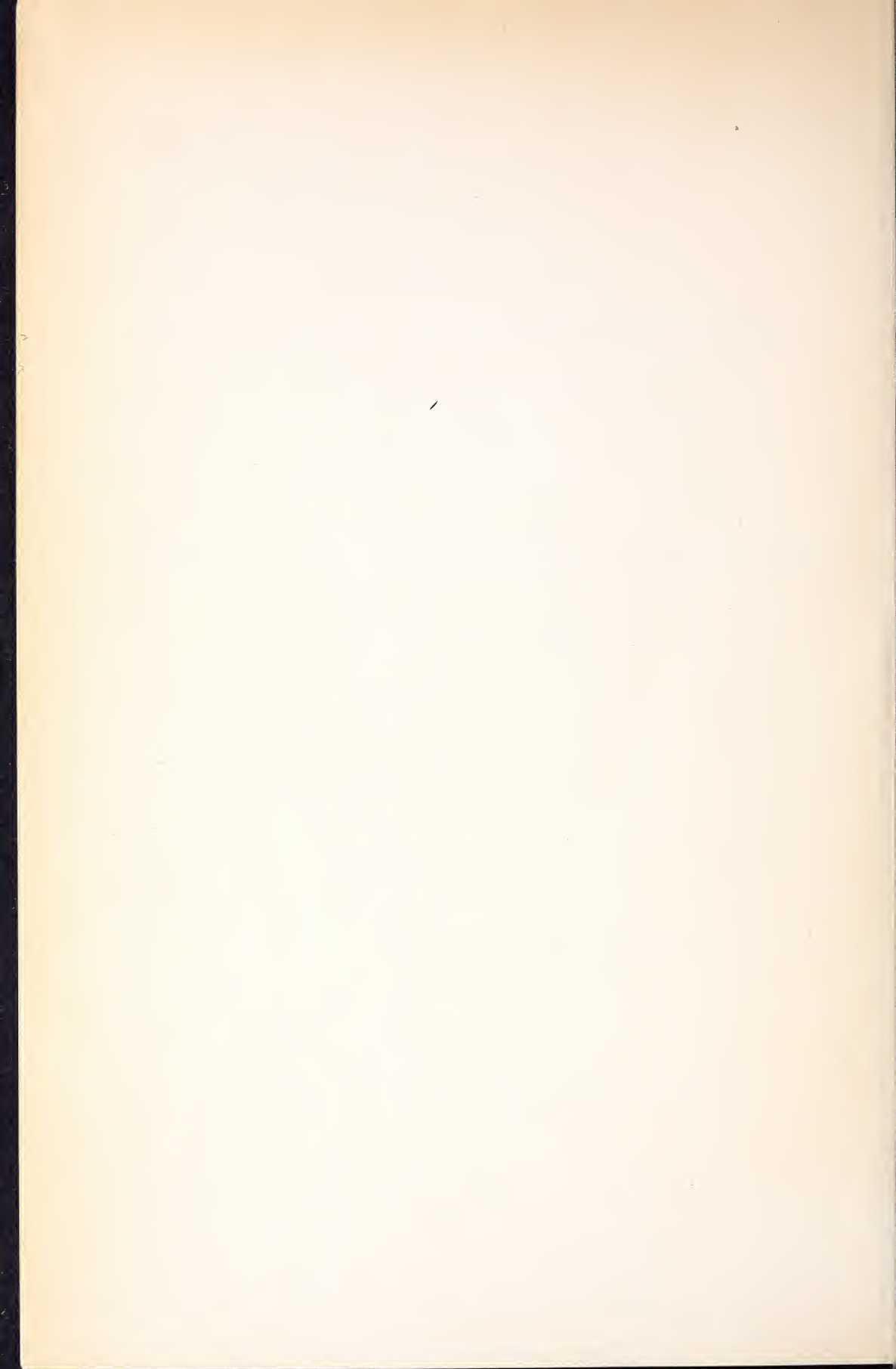
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VI

Le sonar et l'aveugle

Sonar in the blind



#201173

THE HUMAN SONAR SYSTEM

by
Charles E. RICE

In 1749, almost 50 years before Spallanzani began his studies of bats navigating through darkness, Diderot (7) published a comment about a blind man who could judge the proximity of objects by the action of air on his face. Others before and after have been curious about the ability of the blind to avoid collisions with obstacles and have suggested many explanations for this phenomenon. Hayes (15) has described these varied hypotheses and has outlined the early history of scientific inquiry into its sensory basis. An interesting historical analogy exists between the investigation of the senses of the bats and the blind. Spallanzani's research with bats pinpointed their dependence on hearing for avoiding collisions while several early scientists also believed that auditory cues were sufficient to explain the "obstacle sense of the blind" (9). In both cases, the truth was proclaimed, but the skeptics prevailed and the sense of touch continued to be the most common explanation given for the "obstacle sense" or "facial vision". It was not until shortly after Griffin began to resurrect and verify the 18th century work of Spallanzani that the problem of the "facial vision" of the blind was resolved by careful scientific scrutiny.

In the early 1940's, a group of scientists at Cornell University -- Michael Supa, Milton Cotzin, and Karl Dallenbach (38) -- began a series of experiments in which all sensory channels except hearing were eliminated

as not relevant to this "obstacle sense." They concluded that the perception of echoes reflected from the objects approached by the blind provides sufficient information to allow many of these objects to be detected and thereby avoided.

It is curious, as Griffin has pointed out, that the investigation of these two mobility and navigation problems -- one with bats and one with men -- paralleled one another through the years, but apparently were not identified as one and the same by the scientists involved. It was not until Griffin's book, "Listening in the Dark," (12) that the relationship of these problems to one another and to other similar biological systems was thoroughly clarified. One result of all this research was to rename the systems involved, and so terms such as "echo perception," "echo detection," "echo location," and "echo ranging" have replaced "obstacle sense" and "facial vision."

Although the Supa, Cotzin, and Dallenbach study made a great contribution and resolved many doubts, there were important studies of the problem which preceded and followed it. The interest stirred by its publication has fostered many subsequent experiments not dealt with here, but which also contributed to our knowledge of the human sonar system (1, 3, 4, 6, 16, 22, 23, 25, 43, 44, 45, 46). Of immediate interest to us, however, are three studies which have concentrated on the problem of quantitative measurement of man's skill at echo perception.

The first of the modern quantitative studies was reported by Dolanski (8). To our knowledge, Dolanski was the first (1931) to measure how small an object could be detected at a given distance. In his procedure, he moved discs ranging in diameter from 20 to 500 mm toward a stationary subject (S) until S responded to its presence. He found that discs of 100 mm could be detected in front of S while targets as small as 40 mm were noted laterally. The distance at which the target first elicited a response was positively correlated with its size. Several types of target

materials (such as iron, glass, and cloth) were used, but no differences in detection were noted despite these qualitative differences. Dolanski's experiment, although it suffered for lack of some procedural controls, was apparently the first quantitative measure of echo detection in the blind, and preceded the work of Supa, Cotzin and Dallenbach by 13 years. It was, however, not intended to be a quantitative measure of echo detection so much as it was to shed light on the nature of the sensory modality involved in the "obstacle sense," and like its predecessors, it was not sufficiently impressive to convince the skeptics. Similarities between Dolanski's studies and recent ones by Kellogg (20) and Rice, Feinstein, and Schusterman (34) will be noted later.

A second series of quantitative experiments was reported by Kohler (21) after the Dallenbach studies and much of Griffin's work with bats had been published. Kohler was the first to take advantage of the information from these prior works and to attempt to relate echo perception to the growing body of literature about human psychoacoustics. Kohler's was also the initial attempt to stimulate development of an acoustic mobility aid in which the auditory and psychological potential of the human organism is thoroughly considered prior to tackling the engineering problem of building a guidance device. He and his co-workers used a procedure similar to that of Dolanski in concluding that: a) given a proper echo signal and near-normal hearing, virtually everyone can use echo information to detect objects; b) although close to normal hearing sensitivity is desirable for good echo-location ability, it is the sensitivity to small modifications in sounds rather than the absolute sensitivity which correlates well with detection skill; c) brief sound pulses are superior to continuous sounds, and a frequency range of 1-4 kc would be optimal for human echo-location purposes.

In 1962, Kellogg, after conducting many experiments defining the sonar ability of the Atlantic bottlenose dolphin (19) became interested in the

human analogy, i.e., blind persons. He conducted a number of experiments in which he concluded that: a) the sonar ability of human blind Ss was superior to that of sighted Ss; b) the blind could detect changes in distance and perceptual size of a standard circular target; c) differences in surface texture of targets could be discriminated.

In each of Kellogg's experiments, differences in echo intensity could be the single parameter upon which to make these discriminations. The results, however, were sufficiently heuristic to warrant an expanded and more detailed look at the limits of human echo perception. A research program was outlined by Kellogg which had as its goal a systematic basic research approach to the quantitative measurement of human echo-detection ability. Ideally, then, this program would proceed from the challenge laid down by Griffin in Chapter 12 of "Listening in the Dark" in which he expresses the need for a basic research program to explore the possible application of echo-location principles in building an effective mobility device for the blind. "This will almost certainly require extensive experimentation in which various types of sounds are compared under the conditions that are most favorable for making valid comparisons. This means standardized conditions, as few factors as possible varied at one time....rather than a crash effort of human engineering." It is from Kellogg's basic program and Griffin's challenge that this author and his associates have proceeded. The approach to the measurement of human ability at the echo-perception task has been empirical. Few assumptions were made concerning the limits of this ability.

A biological echo-perception system is made up of a number of elements. In its simplest analysis, it may be broken down into the acoustic signal, the physical environment modifying that signal, and the receptor system receiving the echo. Results of some experiments which relate to each of the major variables will be reported in this chapter.

SIGNAL VARIABLES

Although Dolanski (8), Kohler (21), and Myers and Jones (29) demonstrated that an active sonar in which the individual initiates a sound is not necessary, Kohler has shown that echo information is certainly enhanced by an active sonar in which a signal is purposely sent out in order to return an echo from objects.

A variety of signals have been used in previous studies of human echo-location abilities (2, 20, 21, 39). These signals have varied with respect to site of origin, duration, frequency components, intensity, method of production, and repetition rate. In many cases, the theoretical advantages of the bat model have caused investigators to decide upon a repetitious, short-duration signal with emphasis on high frequency components. Some of these, such as one developed by Kay (18), use ultrasonic signals with the echoes brought into the human frequency range electronically. Although Kohler performed some preliminary empirical studies of various electrically generated signals with his Ss, most investigators have designed what might theoretically be the best signal only on the basis of the physical characteristics of the sound.

An alternative approach is to allow S to develop his own signal, using his vocal and oral anatomy, to explore a virtually unlimited variety of possible echo signals. Kellogg (20) used this method in his studies. This assumes that Ss can efficiently "try out" a number of sounds until the one is found that returns what they believe to be the best echo information. This approach takes advantage of the possibility that some people may be able to use one signal better than another, and also the fact that some blind Ss may have developed and practiced their own signals over the years.

The first approach allows one to equate the signal variable for all Ss, but, as pointed out, does not allow us to be very versatile in examining a variety of signal types, and does not consider the possibility that



1. Subject, apparatus, and target in position for minimum threshold experiment.

individual differences exist in Ss' ability to use various signal types. The alternative method allows S to choose what he considers an effective signal, but prevents the experimenter from determining whether differences in skill are due to signal differences or S variables.

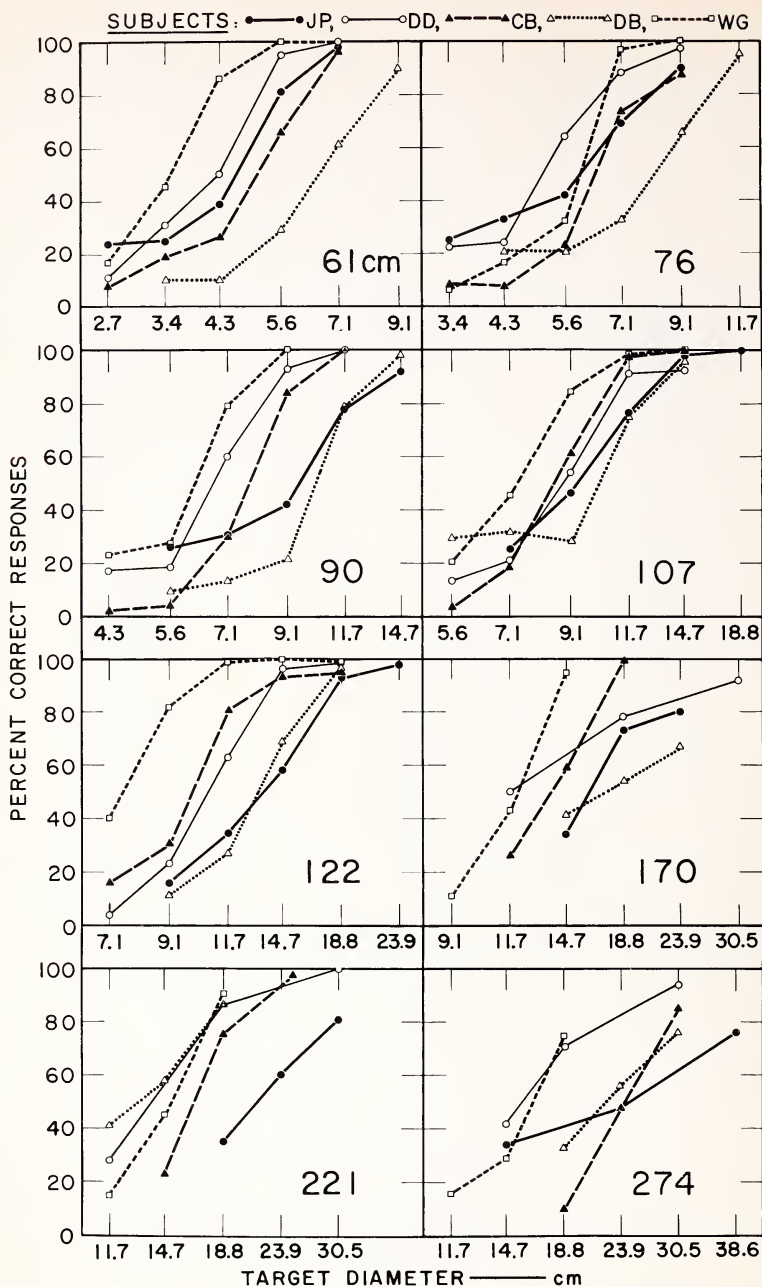
The solution to the problem is to use both methods of signal selection and compare the results. The S has been asked, in the first work reported below, to create his own "best" signal and use it to determine the limits of echo perception unaided by an engineered sound source. Limited only in that it must originate at the mouth, the method represents a sort of test of natural ability on the part of the S which can be compared to results obtained when the signal variables are manipulated.

In the first studies, therefore, Ss were instructed to create any sound they wished from their mouths until they found a signal which they felt brought them good echo information. Once Ss decided upon a signal (usually after a few one-half-hour sessions), they were required to use this same signal in all tests unless otherwise instructed.

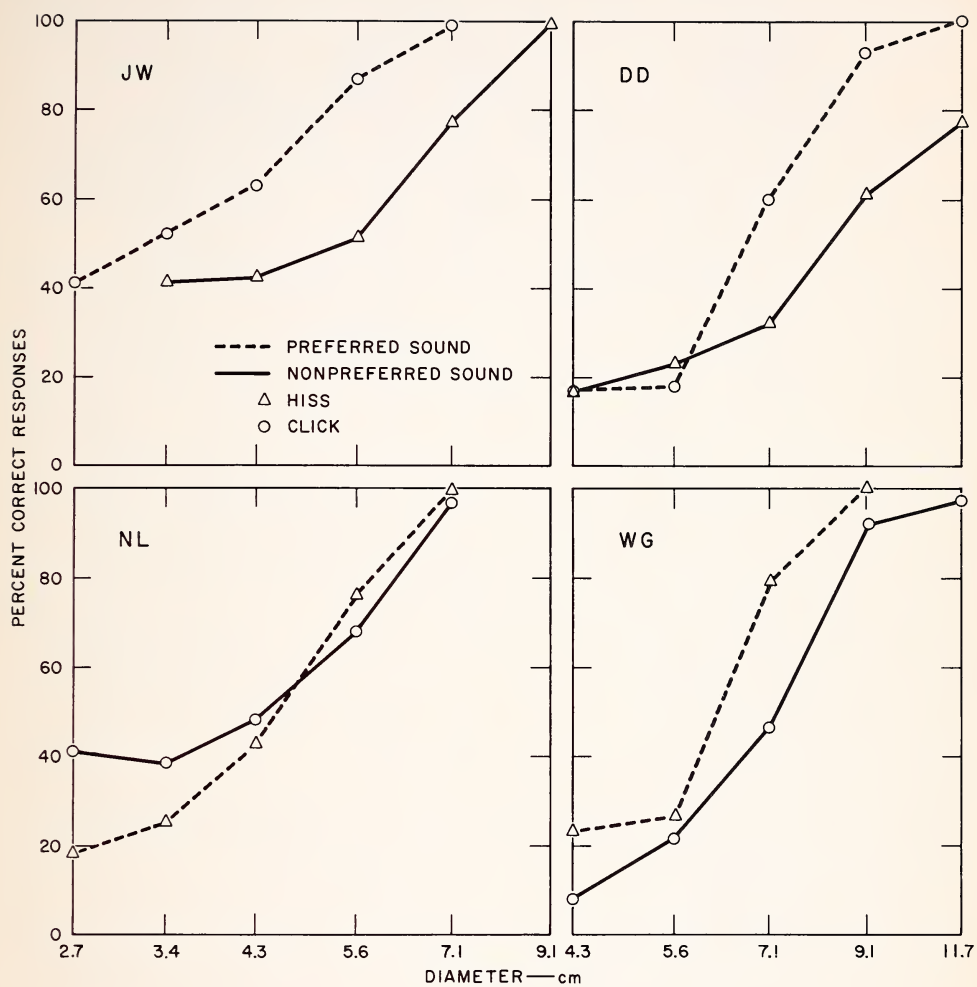
Apparatus and Procedure for Basic Comparative Measurement

The detailed description of the Ss, apparatus, and procedures used in the original study in which S-emitted signals were used appears in an earlier publication by Rice, Feinstein and Schusterman (34). Figure 1 shows S (DB) in position for a judgment in this presence/absence echo-detection task. This experiment determined the minimum size target detectable by each S at several distances. Retest on this same task was subsequently used as a reliability measure and to determine whether manipulation of certain variables affected performance. These retests indicated, for example, that no improvement in performance occurred over a two-year period.

The Ss used a variety of signals, and there were individual differences in performance. This is illustrated in Fig. 2 which shows the percentage of "yes" responses for a series of targets increased in area by 60% steps



2. Percentage of "yes" responses for each S at each distance in minimum threshold experiment.



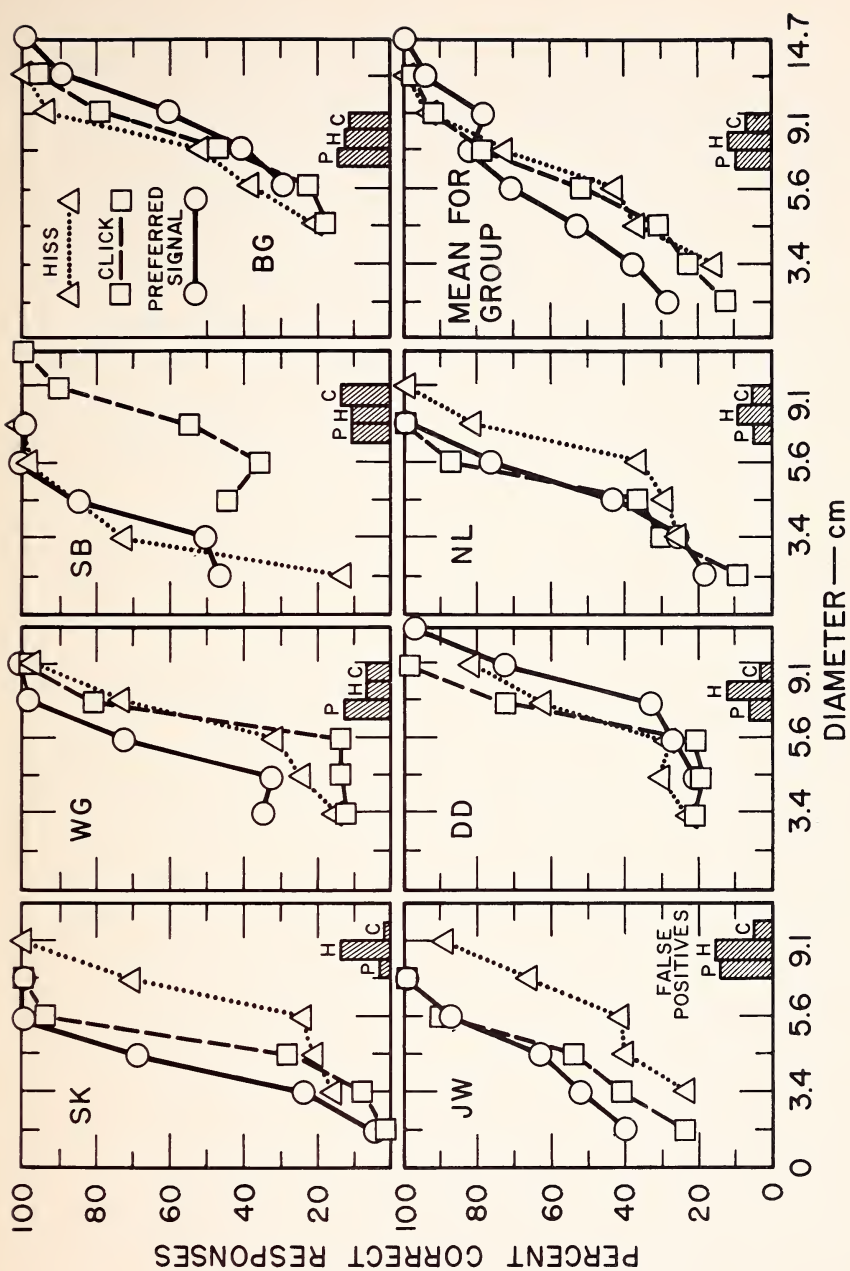
3. Performances using preferred and nonpreferred oral signal.

and presented at several distances. It is interesting that individual differences in performance were consistent throughout, and that the group as a whole is relatively homogeneous.

We have attempted to examine the role of signal variables in the efficiency of performance in several experiments discussed below.

Most of the Ss have arrived at one of two basic types of echo signal, either a form of "hiss" sound or a tongue "click." In order to evaluate the relationship of the preferred signal to ability at the task, an experiment was performed with two pairs of Ss. One pair preferred a hiss-type signal, and the other used tongue clicks. One member of each pair was superior in his echo-detection ability for small targets, while the other member had less ability. The "hiss" pair were asked to change their signal to a tongue click, and the "click" pair changed to a hiss signal. It was hypothesized that if either signal were superior to the other as an echo-location signal, a significant change in performance would be revealed by the comparison. Thus, if the click were better than the hiss, then the click performance of the four Ss would be better than hiss performance and vice versa. Figure 3 reveals that there is no convincing support for this hypothesis. It also appears that the signal chosen by the S suits his needs as well as, or better than, the alternative. Although practice effects could not be equalized precisely, Ss achieved what was believed to be asymptotic performance with the non-preferred signal before commencing the final measurement series. It appears also that even though some decrement in performance is the rule when the signal type is changed, S can still perform reasonably well on the presence/absence task. Significant and usable information can, therefore, be obtained by Ss from either of these signal types.

To carry the comparison of these basic signal types a step farther, and also to assess the degree of individual difference existing in the group, two experiments were conducted in which the performance of all Ss



4. Comparison of Ss' performances using preferred oral signal, electronic hiss, and electronic click signals.

were compared using a uniform signal. In the first, an electrical circuit was developed by which a click signal could be created from a 7.1-cm speaker. This speaker was installed in a 13-cm-long cylinder and mounted in front of S at mouth level. It was aimed at the usual target position. Ss were required to assume their normal testing posture and were permitted to move their heads from side to side if they wished. The electronic clicker which emitted a signal four times per second, contained energy throughout the audible spectrum and was relatively uniform from click to click. The same minimum target size detection procedure was used as before at a distance of 91 cm. Ss could initiate and terminate the clicking by use of a hand-held push-button switch.

In the second experiment, the Ss, apparatus, and procedure were identical with the first, except that a continuous white noise was emitted by the speaker.

The results of these experiments are compared in Fig. 4 with the original S-emitted signal data at a 91 cm distance. It does not appear that the use of either artificial sound source had a unilaterally enhancing effect on S performances. It was expected that if either the "click" or "hiss" were better suited to human echo-location capabilities, differences in performance would be evident when comparisons were made. If a generalization can be made, it is that Ss tended to do as well with the artificial sound which mimicked their preferred sound as they had done with the preferred oral signal. SB, SK, and JW were the least able to use non-preferred forms of the electronic type. The remaining Ss performed about equally well with artificial or natural signals. This test allows us to compare individual performances while holding signal variables constant. No dramatic changes in their performances are noted as a result of the standardization of the signals, and it seems logical to conclude that since signal and target variables were held constant,

the differences in performance are due to differences in ability among individuals.

The physical characteristics of the electronic signals are similar to those developed and used by the Ss. Additional experiments will be conducted in which these data will be used as a standard to measure the effect upon performance of systematic changes in artificial signals.

Acoustics as a Variable in Echo Detection

The physical characteristics of the signals used by the Ss must be described if signal variables are to be related to the behavioral data. These physical properties, when related to the psychoacoustic limitations of the human auditory system, define certain boundaries for echo-detection ability. It is some of these boundaries which this research seeks to define eventually.

The sensitivity of the human ear to sound intensity is bounded between a sound pressure level of about .0002 dyne cm² and 130 dB above that reference level. In a recent article by Dalland (5) it is concluded that "there is little support for the notion that the precision of the bat's acoustically based orientation abilities is.....related to superior absolute hearing acuity." If this is true, then absolute hearing sensitivity may not be the parameter which differentiates between echo-perception abilities of bats and men.

The intensity of a sound decreases as a function of distance from the source. Any signal which is emitted must travel to the echoing surface and return; hence the echo to be detected will be considerably reduced from the outgoing signal intensity. Assuming the sound is radiating uniformly in all directions, its intensity will vary inversely as the square of the distance from the source. Hence, the ability of S to detect the echo of a constant signal will decrease as distance of the echoing surface increases.

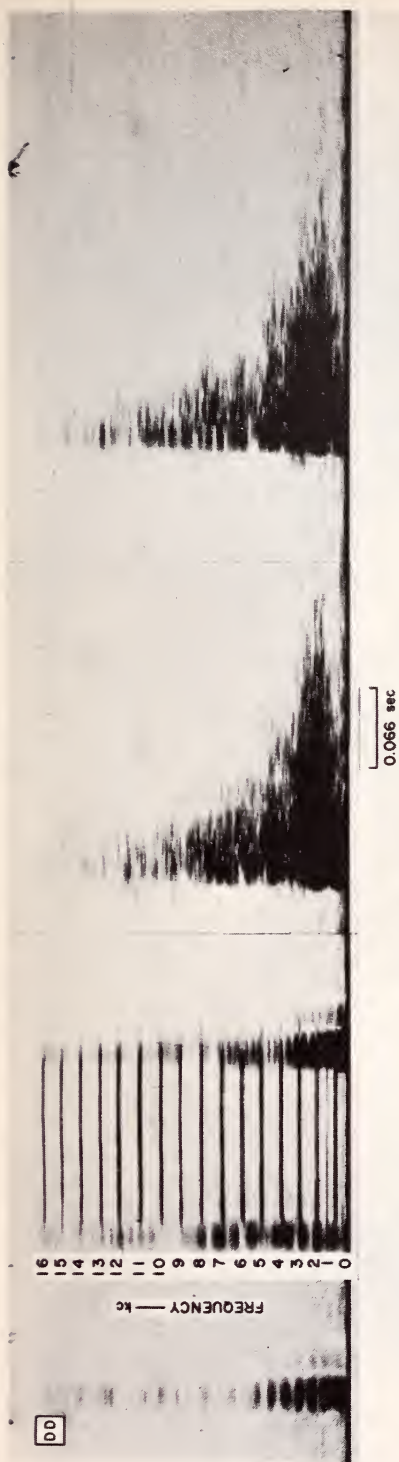
The velocity of sound is approximately 344 meters/sec. The duration of the emitted signal and the distance of the echoing surface, therefore,

determine whether or how much the outgoing pulse overlaps with the echo returning. This is an important factor in determining whether the signal-to-noise ratio will be favorable to detection, and whether human audition will be sufficiently sensitive to detect the echo.

Another acoustic characteristic which limits the echo information received is the spectrum of the signal. The higher the frequency, the shorter the wavelength and the better the reflection of energy from the echoing surface. It is generally assumed that to get a detectable echo from a surface, the wavelength of the sound must be equal to or less than the diameter of the echoing surface. Some investigators question the applicability of this wavelength-to-surface ratio with regard to echoes usable by bats, but the principle is correct, and the shorter wavelengths do produce better echoes.

Assuming that the human ear is capable of hearing frequencies as high as 15 - 20 kHz, and that an object must be at least a single wavelength in size to reflect a usable echo, we can hypothesize limits for the smallest size target human Ss could detect. In this instance, the minimum target size would be 17 - 23 mm. Ss with superior skill can detect a target of 27 mm diameter. Although no formal test of this hypothesis has been conducted, our results seem to indicate that the performance of human Ss is limited by the diameter-to-wavelength relationship, since a 27 mm wavelength would be associated with a signal frequency of about 12.5 kHz, well within normal hearing range for Ss used.

Although these physical principles governing sound waves determine to some extent the requirements for an efficient echo-detection signal, it is the entire auditory system of the organism which plays the primary role. This system sets the limits on how well the echo information arriving at the ear can be used. An example of the interaction between acoustics and audition, and the implication for our current research, are presented later in a discussion of the advantages of hiss vs. click type signals in a shape discrimination task.



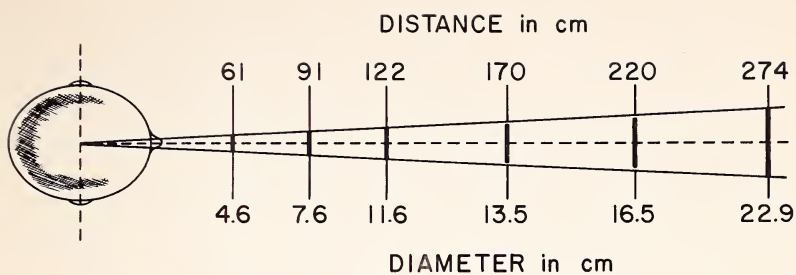
5. Sound spectrograms of typical oral sonar signals.

It may be of interest at this point to look at some of the physical characteristics of the signals developed and used by the Ss as their own sonar signals. As stated before, these fall into two main types: an elongated hiss noise, and some form of tongue click. Sound spectrograms of a typical example of each of these appear in Fig. 5.

The spectrogram provides a graphic representation of the spectrum and duration of an acoustic signal. The horizontal dimension represents time and the vertical dimension shows the frequencies present in the sound. Intensity appears as relative density or darkness of record. The frequency range of the signals shown was from 170 Hz to 16 kHz, and as can be seen, the signals covered this full range. The duration of a tongue click signal is about .025 second.

If an electronic click 4 msec in duration could be generated, for example, it would occupy 138 cm in space. S still would not be able to detect two separate clicks from a target 91 cm distance or less. This is true because at least 2 msec separation is necessary for the human ear to perceive them as two clicks. Therefore, even with such a brief signal, a distance of more than 206 cm is necessary for the separation of the signal and echo to be audible. Data obtained in which considerable signal echo overlap occurs, however, shows no great difference in performance from distances where no overlap occurs. S is capable, therefore, of using the echo information from the click signal whether or not it overlaps.

The hiss signal, it can be observed, has the essential characteristic of a white noise. Since the echo-locating technique used with this signal involves a sound of up to 5 sec duration, the overlap of echo and signal is continuous. Performances of click-using Ss and hiss-using Ss are comparable, as for example, WG and DD, shown in Fig. 2. This seems to

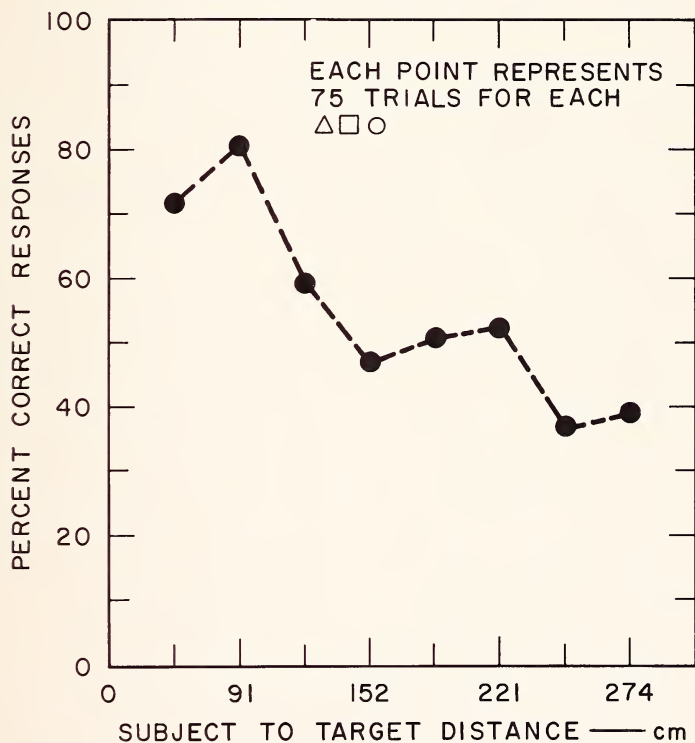


ANGLE = 4.63°

$\sigma = 0.21^\circ$

MEAN THRESHOLD TARGET SIZE

6. Mean 50% target size at each distance tested in minimum threshold experiment.



7. Effect of changes in subject-to-target distance on discrimination of circle, square, and triangle.

indicate that either signal is sufficient to obtain presence or absence information. This apparent indifference to signal overlap may be seen in the experiment on minimum threshold (Fig. 6) in which the calculated mean 50% target is shown for all Ss at each distance tested and appears more likely to be a function of S-to-target distance.

THE ENVIRONMENTAL VARIABLES

When sound energy strikes a physical object, there is some change in its acoustic characteristics. It is absorbed and/or reflected in varying degrees. The amplitude, frequency, and direction of the echo are modified by the collision, and these factors determine what echo information the auditory receptor will receive. In addition to this, an infinitely varying world of sound surrounds the receptor. These environmental factors, which influence human echo perception determine the utility of this form of distance sensing and, as has been pointed out before, a laboratory demonstration of echo-locating ability in humans is quite different from its practical use in the cacophony of the real environment (27).

Directional Reflection

In our experiments to date, we have attempted in most instances to hold the environmental variables constant while exploring the emitted signal or S variables. In one study, however, the effect of a variation in an echoing surface was measured (34). In this study, interest was in the relationship of target surface dimensions to detection. While holding the area constant at 31 cm², we varied the width and length of the target. The four Ss' responses were merely "yes" or "no", i.e., presence or absence, using the same presentation procedures as in previously cited experiments. A circular, a square, and two oblong targets were used at a distance of 122 cm. The oblongs had side dimension ratios of 4:1 and 16:1 and were presented in both vertical and horizontal orientation. Each target was made of flat .050 sheet aluminum and was presented 100 times to each of the

four Ss. It was found that even though the area was constant, the 4:1 ratio oblong was detected less than the square or circle, and the 16:1 oblong was detected less than any of the others. Horizontal or vertical orientation made no difference in percentage of "yes" responses. It was hypothesized that this decrease in detections was due to a loss of echo intensity. There is a specular reflection of the energy away from S's ears as the angle at which the signal strikes the target increases. In order to test this hypothesis, the oblong targets were bent to a radius extending from the center of S's head to the face of the target, and Ss were tested once more. The result of focusing the echo back toward the ear was to increase the number of detections of the oblong targets by a significant amount ($t = p < .01$). Table 1 summarizes these experiments by giving the number of "yes" responses to each of the targets. This study serves, therefore, to demonstrate the importance of the echo surface geometry in the recovery of adequate echo information at the ear.

Qualitative Differences in Echoing Surfaces

As demonstrated above, the presence or absence detection task is influenced by the characteristics of the echoing surface. Beyond this point, however, is the question of whether qualitative attributes of echoing surfaces can be detected by the human ear. Can the ear tell the difference between smooth and rough, between flat and curved, or between wood and metal surfaces? Bats (13), porpoises (19) and sea lions (31) have been attributed with this type of sonar discrimination ability. Unlike Dolanski's Ss, Kellogg's Ss could differentiate between materials of different quality. As previously suggested, however, these discriminations may well have been based on echo-intensity cues due to different reflectance and absorption characteristics. Qualitative differences would be recognizable on the basis of a distinctive signature or sound which could be distinguished from nearly all others, much as a familiar word can

Table 1

Total Correct Detections for all Subjects

Target Shape	Flat	Curved	Flat
Circle	341	340	354
4 x 4	369	338	367
2 x 8 Vertical	317	323	314
2 x 8 Horizontal	313	335	334
1 x 16 Vertical	90	227	87
1 x 16 Horizontal	105	161	89

Table 1. Total correct responses for all Ss using flat targets, curved targets, and a control series with flat targets.

be recognized whether it is spoken loudly, softly, quickly, or with an accent. Qualitative discrimination involves, then, formation of an auditory concept which is akin to the constancy phenomenon of the visual modality. It has been a temptation to leave the tedious and time-consuming tasks involved in the threshold studies in order to discover whether humans can discriminate between a moth and a leaf, or between horsemeat and herring. To our knowledge, even our most advanced forms of radar and sonar have failed to yield clear distinction between, for example, a whale and a submarine. An interesting introspective report has recently appeared, however, in which an observer, using Kay's mobility aid, reports being able to make many qualitative distinctions with the echo information from the device (11).

Our closest approximation of this task has been a preliminary and unfinished study of shape discrimination. In this experiment, Ss are presented with targets of three different shapes having equal areas. The shapes used were circle, square, and triangle. To date, four Ss have been able to make the discrimination among all three targets with 80% accuracy. Others who have worked at the task have been able to discriminate between two of the targets, but not among all three. WG has been tested under a number of conditions to determine whether an auditory concept of the shape has been formed, and such does not seem to be the case. Figure 7 illustrates, as an example, the effect upon his performance of increasing S-to-target distance.

It must be remembered that this is a preliminary result, presented here only as an example of the more qualitative discriminations hypothetically possible. Learning factors and the variables differentiating between those who can perform the discrimination and those who can't must be pursued further. Concerning this latter point, an hypothesis is being tested as to why WG is superior to some Ss in the shape discrimination task. The most apparent difference between WG and the others is in the type of

Table 2
Personal Information About Subjects Used in These Studies

S	Degree of Blindness	Cause of Blindness	Age at Loss of Vision	Present Age Yrs.	Educ. Yrs.	Verbal WAIS	Preferred Travel Method	Type of Sonar Signal Preferred
CB*	Total	Glaucoma	6	22	14	136	Cane	F sound
WG	Slight light Perception	Illness	25	32	20+	145	Dog	Hiss sound
DD	Total	Injury	11	25	12	122	Cane	Tsk Tsk
DB	Total	Glaucoma	3	27	16	139	Cane	"Six, seven, eight"
JP	Total	Optic nerve atrophy	7	27	13	107	Dog	Lip smack
JE	Total	Injury	16	41	16	126	Dog	Hiss sound
AG	Total	Hereditary tumor	15	20	10	76	Cane	Hiss sound
JK	Total	RLF	Infancy	20	15+	135	Cane	Tsk Tsk
JW	Total	RLF	Infancy	22	16	132	Cane	Tsk Tsk
NL	Slight light Perception	RLF	Infancy	18	11+	104	Cane	Hiss sound
DN	Total	RLF	Infancy	17	11+	116	Cane	Tsk Tsk
SK	Total	Retinal blastoma	Infancy	23	16	135	Cane	Tsk Tsk

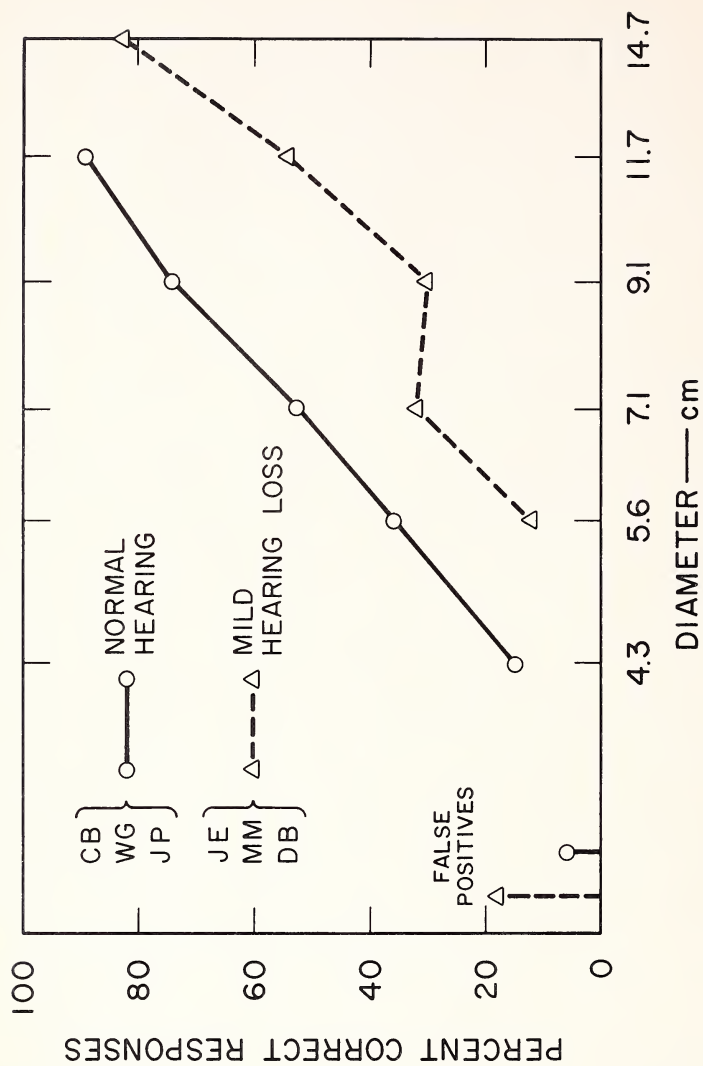
* Deceased

+ Still attending school

Table 2. Characteristics of the blind SS used in the research.

signal used. WG uses a hiss, while the unsuccessful Ss all use click signals. WG has also been more successful than a click S in a task requiring Ss to "find the left edge of the target," (32). We hypothesize that the hiss signal provides more precise information to S when the corner of a target or object first reflects an audible echo. The hiss provides a continual echo feedback, while the click, being pulsed 3 to 4 times per second, may be less effective in picking up the first detectable increase in echo intensity from the leading edge of an object. It remains to be seen whether other hiss Ss provide substantiating data. If they do, this could provide insight into how and why some biological organisms developed longer duration signals.

If shape detail can be obtained in this manner, it is conceivable that the relatively long signals of, for instance, the Rhinolophid bats and some others, are an adaptation of their signal for this purpose (28). This, too, might account for the increase in pulse repetition rate of other organisms when the presence of a target is detected. As the organism is approaching the prey or obstacle, a rapidly increased repetition rate on approach creates, in essence, a continuous overlapping feedback of information much as in the edge-finding hiss, and allows the sonar to keep track of the echoing object. This sort of hypothesis requires that a highly directional signal be used for obtaining precise information. In the present study, the specular reflection from the plane targets used helps to account for the precision of WG's directional judgment in finding the left edge. The directional influence of reflecting surface on the signal is evident, and the most favorable echo from the target surface occurs over a relatively small angle from source to reflector to receptor. Thus, with a continuous signal, the increase in echo intensity as S moves his signal close to the target is rapid when this angle is reached. The click, on the other hand, is limited in duration and may occur immediately before or after the critical angle is reached.



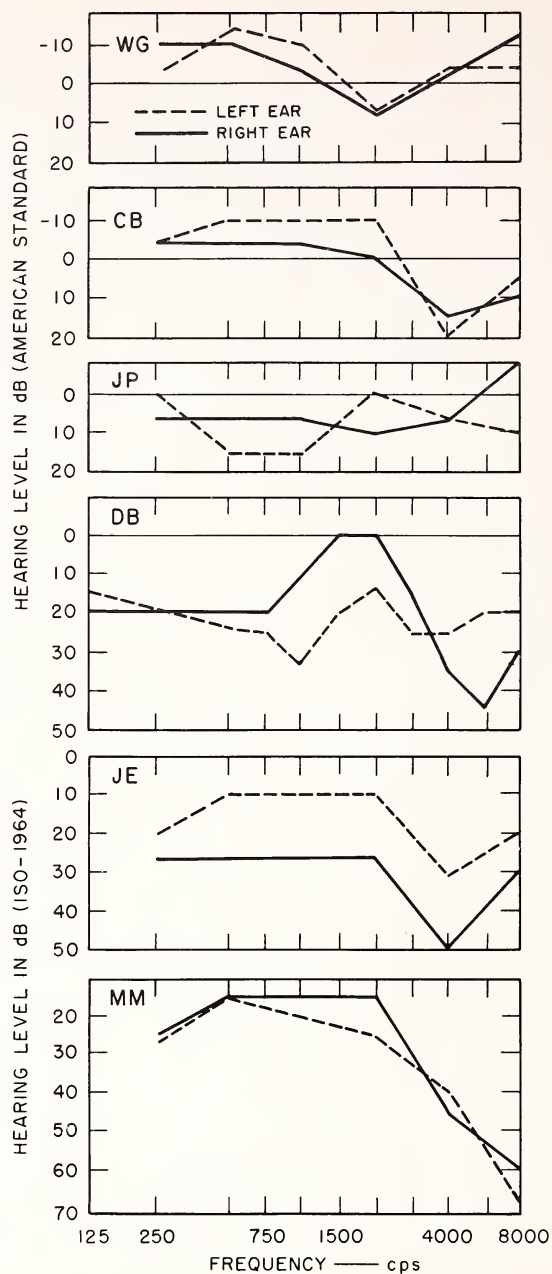
8. Comparison of performances of S_s having normal hearing with those suffering mild hearing loss.

INDIVIDUAL DIFFERENCES AS A SOURCE OF VARIABILITY

In the analysis of human echo-perception abilities, there are differences in performance which are related to differences among individuals. These may be physiological differences in the auditory portion of the central nervous system or variations of pinna configuration, ear separation, abnormalities due to disease or injury, or in shape of the mouth when a vocal signal is used. Other sources of individual differences may be psychological, such as attention, motivation, intelligence, and personality. Experience and learning, as determined by duration of blindness and amount of practice at the task, must also be considered as possible contributors to differences in demonstrated ability.

Hearing Sensitivity

Previous work (particularly Kohler's) has indicated that being able to hear slight changes in a sound is more important to the perception of echoes than is good absolute sensitivity. All Ss tested in our laboratory have had a routine audiometric examination. These tests were conducted at a speech and hearing clinic under standardized conditions. The standard audiometric examination covers a frequency range of 250 - 8000 Hz. Higher frequency sensitivity norms have not been standardized, due to technical problems. The audiograms of all but three Ss (DB, MM, JE) used in our study indicated hearing to be within normal limits up to 8000 Hz. In these three instances, however, moderate sensorineural hearing loss was found. The mean performance of these three Ss on the minimum size threshold test is compared with that of three Ss with normal hearing, as defined by a professional audiometrist, in Fig. 8. The graph is plotted using using points where two or more Ss in each group were presented the same target sizes. The audiograms of these Ss are shown in Fig. 9. These data seem to indicate that for this type of task, relatively good hearing is necessary for good performance. This means that although the basic discriminations may be between two audible sounds, the relative sensitivity



9. Audiograms of Ss having normal and subnormal hearing. Deviations 20 or more dB from zero are abnormal.

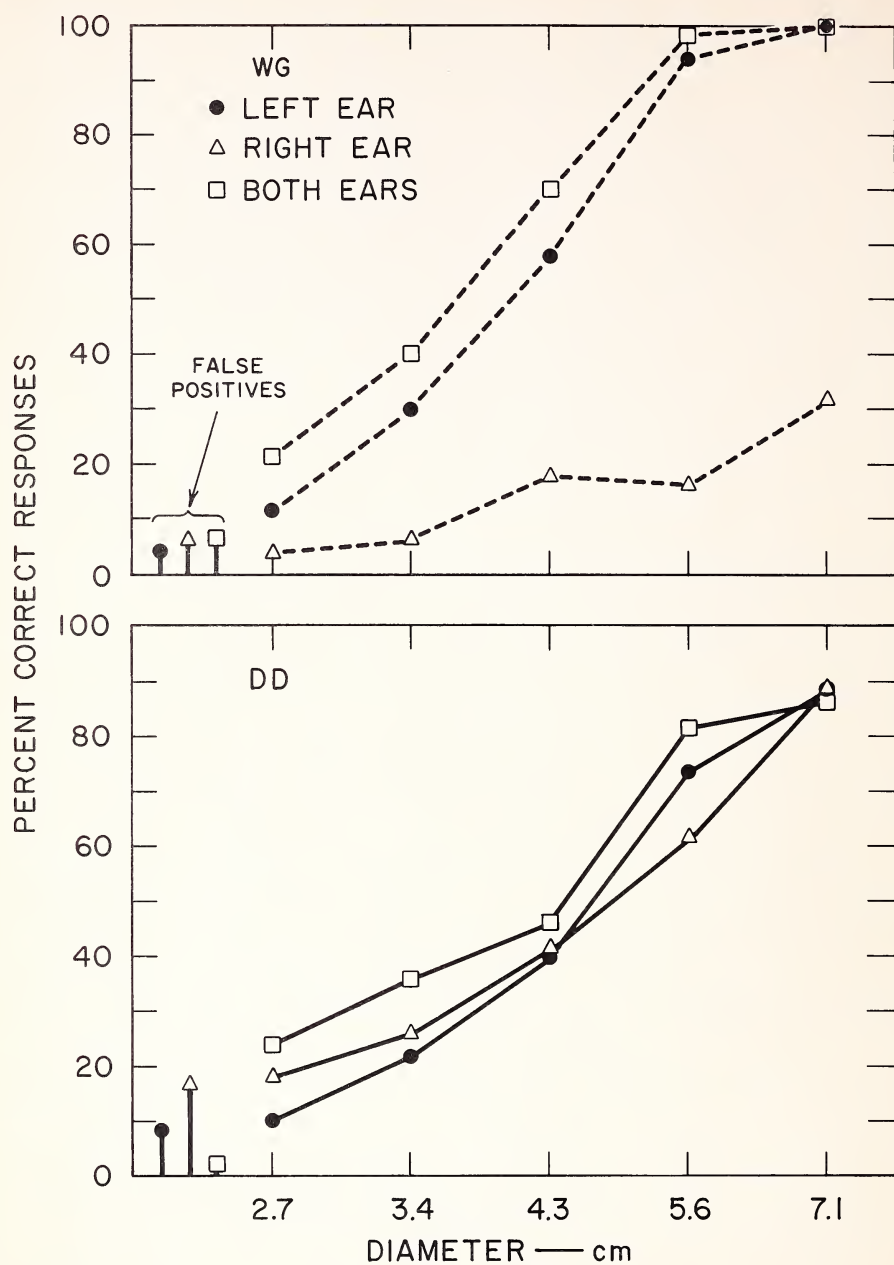
of the ears has a measurable effect on performance. In order to detect small targets, as in our example, it is necessary to have good enough high-frequency sensitivity to perform the comparisons involved for the particular echo-detection task. We must conclude, therefore, that echo location is possible only if the echo information is in the audible range of the S; since the most efficient echoes are of high frequency, there is an obvious advantage to having good high-frequency sensitivity. When the signal and echo characteristics are sufficiently audible, then the difference threshold factors come into play. We have not yet encountered Ss with normal hearing sensitivity who cannot perform satisfactorily in an echo-detection study.

It is interesting to note that where larger targets are used, the less sensitive group performs nearly as well as the high-frequency hearing group. Since the higher frequencies of the echo are the only ones efficiently reflected from the smaller targets, and since the three less sensitive Ss are weak in the high frequency range of hearing, their problem in detecting the small targets is understandable. The improvement in performance occurs because echoes reflected from the larger targets are in a frequency range detectable by these Ss.

These results can, therefore, be taken as support for earlier studies which have contended that perception of high frequency sounds is correlated with echo location and mobility (4, 35).

Binaural versus Monaural Echo-Detection Thresholds

In all previous studies of the echo-detection task, S has presumably used both ears. A number of observations of Ss while they worked, and some subjective reports, indicated to us that monaural echo detection is possible, and that with some Ss one ear might serve as the dominant or preferred ear when listening for target echoes. We had, for instance, noticed that JW directed her signal as much as 45° to the left of the target in a presence/absence experiment. Thus, her right ear was closer



10. Comparison of Ss' performances using either and both ears.

to the target, while her left ear was essentially masked to high frequencies of the target echo by her head. Other Ss reported that they felt one ear or the other played a dominant role in echo detection. To test whether these observations could be substantiated experimentally, two Ss were tested on the minimum threshold experiment at a 61 cm distance. All apparatus and experimental methods were the same as those in the original study except that one ear or the other was effectively masked from ambient sounds by use of a Sharpe HA-10 headphone. This headphone has an advertised attenuation of 40-dB ambient noise at 1000 Hz. Subsequent control tests with the earphones on both ears substantiated their effectiveness in preventing echo detection. Each S was given 50 trials for each target and 50 no-target catch trials. The targets used were those of the original 61 cm threshold measurement. Comparison threshold measurements were made with Ss using both ears, then the left ear, and then the right ear. Since both Ss were well trained and had had long experience in the task, it was felt that practice effects would not obscure any deficits in performance due to the monaural condition. The data obtained in this experiment are illustrated in Fig. 10 in which each S's performance under monaural conditions is compared with his binaural performance.

These data indicate that WG was severely handicapped in his ability to use his right ear. The audiogram for WG shows normal sensitivity in each ear. It seems, therefore, that the left ear must have been used as the primary source for echo perception. It does not seem likely that one ear would become so perceptually tuned to a task that the opposite ear, though equally as sensitive, would not perceive the information when called upon. A recent article by Fisher (10), however, suggests that "ear dominance" may exist in some persons. This would seem to necessitate a central control over the selection of auditory input stimulation to a single ear. A simpler hypothesis might be that perception of targets is based on echo-frequency

information above 8000 Hz, and that although audiograms of WG before and after this test show excellent hearing up to 8000 Hz, he may not be so sensitive to higher frequencies.

Other Individual Differences

A number of characteristics of blind Ss used in the program of research reported here appear in Table 2. For example, the question of intelligence is often raised in relationship to echo-perception ability (42). As can be seen from the table, our sample has been largely above average in intelligence. We have not, therefore, been able to link intelligence to excellence in echo-detection performance. A larger number of Ss and a more normal distribution of IQ scores would be necessary to test such a relationship. We are inclined, at this point, to doubt that intelligence test scores will correlate highly with an objective measure of echo-location ability. However, whether a person having the ability to use echo information uses it or not may correlate with intelligence test scores. It seems likely that at the lower extremes some relationship would be found. Within normal limits, however, we have found considerable individual difference in performance which does not appear to be best explained in terms of differences in intelligence.

Table 2 helps emphasize a problem in attempting to treat the blind population as a S population. It will be noted that there are only two nearly homogeneous traits shared by the group. None have more than the faintest light perception, and each of them is regarded as a "good traveler." "Good traveler" means that they manage to travel well enough to pursue work, school, and recreation activities despite being blind. It is this ability to get about which might lead to the hypothesis that this group would be superior echo detectors to other "poor travelers" and to a sighted control sample.

Experiments now being conducted are aimed at testing this hypothesis. To date, insufficient evidence is available to present for comparison. We

can say, however, that several sighted Ss have developed effective sonar signals and one, at least, has demonstrated skill equal to any blind S yet tested on the presence/absence experiment.

PSYCHOACOUSTICS

The interaction of acoustic energy with the auditory perceptual system is called psychoacoustics. To study how humans respond to the parameters of acoustic energy is an extremely complex undertaking. The contribution of many psychologists, physicists, physiologists, engineers, anatomists, and mathematicians have established a number of factors basic to the interpretation of studies such as ours. Some of these findings place limits upon what can be expected from human echo perception. Most of the studies which define the limits of the human auditory system do so within the framework of precisely controlled experiments. The interaction of a wide variety of psychoacoustic events occurs, however, in echo perception.

We cannot ignore the principles which have been given us as guide lines for predicting human ability in these experiments, but these guide lines must be related to the empirical data obtained in the echo-detection studies.

If two clicks occur closely spaced in time (2 msec or less), the second of the two sounds will not be heard, particularly if the first is appreciably louder (40,41). This precedence effect has been cited as a reason why human echo perception of close objects would be poor. Yet we have shown that Ss can and do detect objects when an echo is returned to the S in less than 2 msec (Fig.2). In this condition, the signal and echo occur in less than 2 msec and overlap one another. Because they overlap, the effect is one of augmentation and the ear hears a louder or at least slightly different signal than when no target is present. Thus, difference thresholds for intensity and for frequency are crucial to near-object

detection. Second, if a sound arrives at one ear as little as 30 sec prior to reaching the other ear, information as to the position of the sound source in space can be localized. Thus, if the echo is sufficiently loud to be heard and the arrival time at the two ears is slightly different, the location of the object may be perceived in addition to its presence. A recent study has shown that this localization of echoing targets by blind Ss is relatively accurate (32).

A more thorough consideration of the psychoacoustic factors which influence echo-detection ability is beyond the scope of the present paper. There are several references which consider this specific problem as well as psychoacoustics in general, and the reader is referred to these sources (14, 17, 24, 26, 27, 30, 36, 37, 40, 41). A complete understanding of the echo-location process in animals would also be dependent on knowledge of the psychoacoustic characteristics of the organism.

The research findings reported here are empirical evidence of what human Ss can do under controlled laboratory conditions. It must also be reiterated that this report represents very preliminary exploration of the limits of human echo-perception abilities. As with most research, more questions have been raised than answered, and much that seems obvious remains to be demonstrated.

SUMMARY

A systematic investigation of human ability to detect objects by an active sonar technique has shown: (1) many kinds of sound emission can be used to detect objects; (2) repetition of measurements yields reliable performances from trained Ss; (3) small changes in target size and/or distance produce observable and orderly changes in performance; (4) there are individual differences in ability at the task. Echo detection ability follows lawful and readily observable change as signal, environmental or receptor variables are manipulated.

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Footnotes

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ABSTRACT

A systematic investigation of human ability to detect objects by an active sonar technique has shown: (1) many kinds of sound emission can be used to detect objects; (2) repetition of measurements yields reliable performances from trained Ss; (3) small changes in target size and/or distance produce observable and orderly changes in performance; (4) there are individual differences in ability at the task. Echo detection ability follows lawful and readily observable change as signal, environmental or receptor variables are manipulated.



ENHANCED ENVIRONMENTAL SENSING BY ULTRASONIC WAVES

by
L. KAY

1. INTRODUCTION

The ability of blind people to sense their environment has been studied for many years. The information made available from the many experiments is invaluable in terms of subjective ability but it is now generally recognised that the unaided natural performance of the Blind is very limited. At the same time it is also recognised that any form of enhanced auditory environmental sensing which may be devised should use the sense of hearing in its most natural form. Beurle (2) in 1950 and again Kohler (7) in 1964 worked on this basis by producing "clickers" which emitted pulses of audible sounds in the form of high pitched clicks. Similar sounds can be made by the tongue or snapping fingers; some blind people use steel tips on their shoes or tap a cane. The "clickers" differ considerably in principle to the naturally made clicks, particularly sounds made by the mouth, although no mention appears to have been made of this.

Anyone making clicks or similar sounds hears these clearly, and any echoes produced by the environment simply modify the quality. This is noticeable when comparing the sounds in an anechoic chamber with those in a reverberant room such as one without floor covering or drapes. The sound generated is the

same but the sound heard is quite different. Under these extreme conditions the untrained person would easily be able to say which was which even when deprived of all other cues. He would not however readily be able to describe the reverberant room, and most certainly could not detect the presence of an object which may be between him and one of the walls. It is even doubtful if he could walk up to a wall and stop just before bumping it. Many blind people who possess normal hearing ability can position walls with a fair degree of accuracy and some will even estimate the dimensions of a room with uncanny skill. An object between them and a wall can often be detected provided it is greater than a minimum dimension and above chest height or thereabouts. The difference between the untrained and the trained (usually self trained) is that the trained has learned to interpret the subtle change in quality in the sound, or he may be able to observe the returning echo against the background of his own sound since the two may overlap.

The same subjective result is not observed with the clickers of Beurle or Kholer. Beurle's unit was in the form of a torch and the pulsating crystal was placed in a cone so that the sound beam was relatively narrow. In free space, the clicks could be heard quite clearly by the user, even when the torch was pointing into space, and they were unpleasantly loud when directed towards the head. When an object was in the sound field the echo from the object usually dominated the sound from the torch, as heard by the user, and he had the sensation that the object itself was making a click - or there was a clicker at the

position of the object. The user did not observe the clicks from the torch at the same time unless special attention was focussed on this and even then it was not always possible depending upon the size of the object. Kohler's unit emits sound over a wide arc and is carried on the chest. A shield reduces the sound reaching the ears directly. Again the impression is the same. Objects appear to be making the clicks and the untrained person can hear this effect. It is therefore possible to determine the position of objects with the same degree of accuracy that natural sounds are positioned.

These two devices are therefore a considerable improvement over generating sounds naturally but devices making audible sounds which the general public can hear are objectionable. In addition they are less effective in areas where there is a high noise background. Not all objects can be detected and those which are detected cannot be recognised with a reasonable degree of certainty even after long experience because the variation in quality of the echo is not marked. There is, however, a noticeable variation when the objects are large compared with one wavelength and are markedly different in their reflecting properties. A hedge is noticeably different from a wall.

Both devices on the other hand are using the sense of hearing in its most natural form and are therefore likely to be optimal in this respect - the main argument for their use. This is why objects appear to make the sounds; the binaural perception of the echos gives true localization.

The mechanism whereby the auditory channels do this

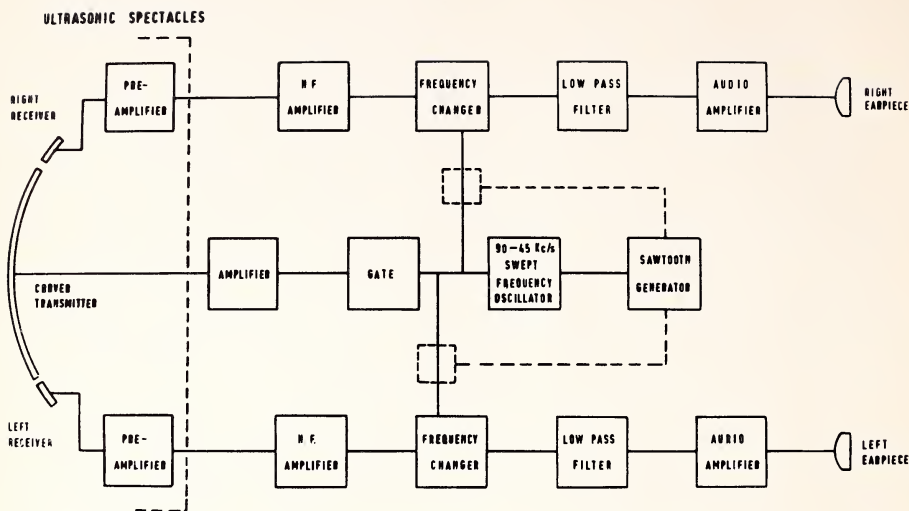


FIG.1 BINAURAL ENVIRONMENTAL SENSING FOR THE BLIND

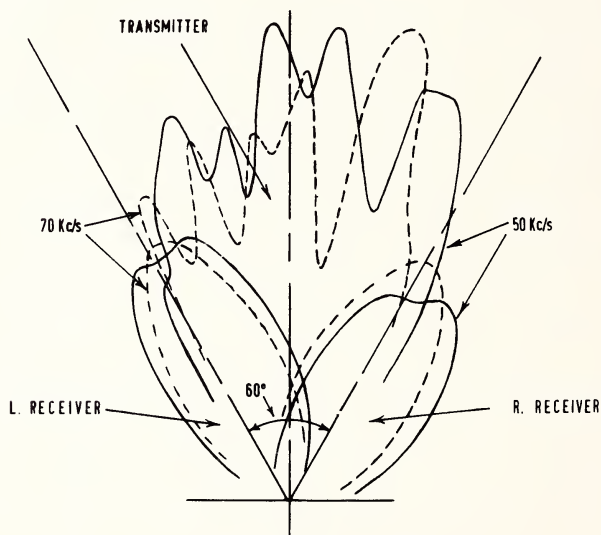


FIG.2 POLAR RESPONSE OF TRANSMITTER & RECEIVERS

is not fully understood, and various theories have been advanced. Batteau (1) emphasised the use of the pinna, whereas Cherry (3) makes most use of the neural correlates. All that can be said with certainty, is the basic information which enables this to be done is present in the two channels.

It may be that if the same information is presented in a different auditory form, the neural channels will adapt to the new display after a period of learning.

This paper describes what is believed to be the first alternative approach to the generation of audible sounds which at the same time uses binaural perception. The results show interesting possibilities for the Blind and at the same time throw some light on the apparently remarkable ability of bats and marine mammals to use their "sonar".

2. BINAURAL PRESENTATION OF F-M ECHO-LOCATION SIGNALS

The system uses the same principle as the Monaural
(4)
Sonic Aid for the Blind but utilises a wide angle transmitter and two wide angle receivers spaced apart a distance approximately the same as the spacing of the ears. One receiver is coupled to the left ear and the other to the right ear. The arrangement is shown schematically in fig.1.

When insonifying a wide arc of 60° or more in order to obtain a wide field of "view", and at the same time varying the transmission frequency through an octave band, a special form of radiator is required. This is because the intensity of radiation should remain approximately constant throughout the arc. A convenient way of achieving this is to use a curved radiator

having a radius of curvature greater than 8 wavelengths. The resultant beam is approximately a continuation of the sector formed by the curved surface and the centre of curvature, but the intensity of radiation over the sector varies according to the wavelength. A typical radiation pattern formed by an experimental curved transducer is shown in fig.2. It will be observed that the peaks at one frequency may coincide with the troughs at another frequency.

The two receivers are designed to cover the arc of emission in a particular way. Two disc transducers are used to cover the arc of transmission by splaying their axes an angle equal to the arc of radiation as shown in fig.1. The sensitivity of reception varies considerably over the arc as seen in fig.2 and it will be noticed that signals from the right, say, will be stronger in the right receiver than in the left. Signals from ahead are somewhat weaker than would be obtained on the receiver axes. The polar response also varies with frequency.

Vertical radiation and reception varies with frequency and is similar to the receiver response in azimuth.

The variation of frequency with time is shown in fig. 3. The pitch of an echo signal is proportional to distance and a note of 3 Kc/s corresponds to 10 ft. in the arrangement used. From fig.3. it will be seen that the audible echo note is interrupted during the fly-back period because the high difference-frequency is rejected by a low-pass filter. During this period several transient states arise and, if not specially suppressed, can be heard as clicks in addition to the echo signal. To

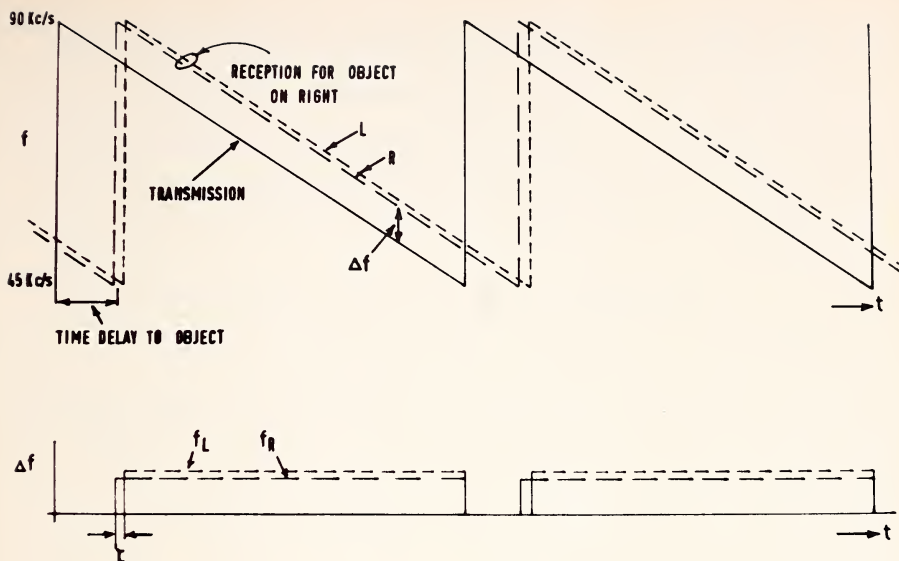


FIG.3 FREQUENCY-TIME RELATIONSHIP

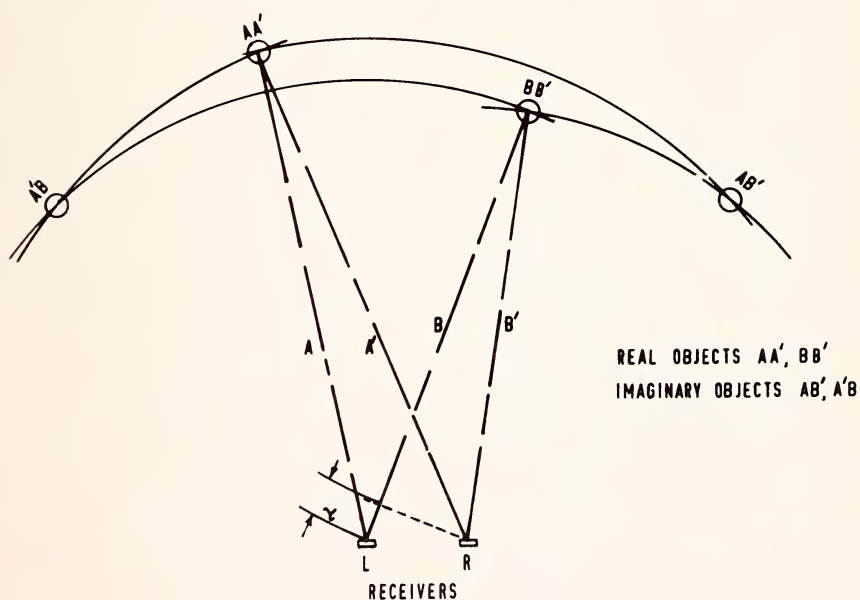


FIG.4 SIGNAL AMBIGUITY

eliminate these completely the transmission is interrupted during the flyback period. The connection between the frequency swept oscillator and the two modulators (shown dotted in fig. 1.) is not normally interrupted as this alters the system behaviour. (See section 4.3)

Signals arriving from an object directly ahead reach both receiving transducers simultaneously and, for an ideal reflector reradiating the wave energy equally towards each receiver, the outputs from the two channels are identical in all respects. The time of arrival, the pitch of the audible note, and the amplitude modulation as well as the phase are the same. This is the only condition for identical audio outputs and depends as much upon the dimensions and shape of the reflector as its position. An object to the right of the ahead position, as shown in fig.4, is further away from the left receiver than from the right. The time required for a reflected signal to reach the left receiver is therefore slightly greater than the time to reach the right receiver. In this system, whether or not the transmission is interrupted, the signals arrive as long pulses with short intervals between. (See fig.3). There is therefore a time-difference τ between the two audible outputs, and because the spacing of the receivers is similar to that of the ears, this time-difference is similar to that experienced when listening to natural audible sounds. In addition, because the system is arranged to convert distance (or time) to an audible frequency, the pitch of the echo note is also slightly different in each output. The note in the left ear is higher than in the right for an object on the right. For example,

if the difference in distance between the object and the two receivers is 1 inch, corresponding to an angle of about 10° off the ahead axis, and remembering that 3 Kc/s corresponds to 10 ft. (20 ft. travel distance) the difference in frequency is

$$\frac{3000 \text{ c/s}}{20 \times 12} = 12.5 \text{ c/s.}$$
 Neglecting second order effects, this

difference in frequency is independent of distance to the object and is only a function of direction. For angles up to $\pm 45^\circ$ of the ahead position it is also approximately linearly related to angle. A simple experiment with two audio oscillators and a pair of independent headphones amply demonstrates that a person with normal hearing can easily detect a change of 10 c/s between an audible note in the left ear and one in the right.

If the receivers were directed ahead, their polar responses would overlap almost exactly, (except at close distances) and the amplitude modulation of the echo signal would be the same in each channel, displaced by the time-difference of arrival of the two signals. When the receiving transducers are splayed 60° , as shown in fig.1, so that the left one is directed along the left edge of the transmitting arc and similarly for the right, the amplitude modulation of the two echos is different (again assuming an ideal reflector). This is because the polar responses for a specified direction are different and vary with frequency. The signal in the right receiver will also be of larger amplitude. There are therefore four direction cues (1) time-difference of arrival, (2) frequency-difference, (3) amplitude difference, and (4) amplitude modulation. Phase difference is not relevant now

since it is a constantly changing parameter owing to the difference in frequency between the two channels for all except the ahead direction.

Complex object situations produce highly complex signal patterns. These contain the same basic distance and direction information as the single ideal reflector for each reflecting element in the spatial pattern. A pattern transformation thus takes place from spatial co-ordinates to a complex frequency spectrum and the neural system is subsequently required to retransform from the auditory pattern back to the spatial co-ordinates in order that perception of the immediate frontal environment may be possible.

3. SOME THEORETICAL CONSIDERATIONS

3.1 The Monaural System

Before discussing the subjective experiments with the binaural system, a brief examination of the theoretical limitations is necessary. It is well known that the resolution of an echo-location system (or in fact any system using wave energy is limited by the receiving aperture. In general, the greater the number of wavelengths across the aperture the better the resolution. It also follows that the higher the frequency the greater is the resolving power of the aperture being considered.

The same must apply for the binaural perception of an ultrasonic echo-location system, even though the signal analyser is the human neural system. The ultimate performance may however be better than could normally be expected of a machine because

of the self-adaptive nature of the human analyser. This has been found to be so with the Monaural Sonic Aid for the Blind which is in the form of a torch, using a narrow beam of about 10° . It was thought of initially as a simple one-dimensional system, although two dimensions were to be obtained kinesthetically by hand scanning together with a capacity to memorise signals. This would enable a user to picture in his mind the immediate environment. It is found that the variation in the amplitude of an echo signal as the beam of ultrasound traverses an object gives some indication of its dimensions. Whilst the beam is stationary, however, only one dimension (distance) is perceived. A stationary beam of course is of little use to a blind person and movement must be considered whether it be due to a scanning action or forward progress - or both. This has not been discussed in the literature (5)(6), since the complexity of the signals received under these conditions were thought by many to contain too much information for a blind person to utilise at any one instant. This is still true, but experience now shows that redundant information can be neglected. At the same time it has been found that complex information is useful under certain circumstances. Reference has been made to "side vision" by one skilled user, and a superficial analysis of the information suggests that he is making use of the difference in Doppler frequency shift between signals received along the line of progress and signals to the side of this, together with the rate of change of amplitude. The greater the distance an object is from the line of progress the greater will be the relative change in signal characteristic.

The audible signal can in fact be expressed in simple mathematical terms which will show the degree of complexity involved.

3.1.1. Angular Rotation

Let the angular response of the torch be given by $F_1(\theta, f,)$ i.e. a function of the angle off the axis of the beam and the frequency of emission and reception. The combined transmit and receive response is then $F_1^2(\theta, f,)$. If the output of the receiver under stationary conditions is expressed by $AF_2(d)$ i.e. a function of the distance, multiplied by a constant which is determined by the reflecting characteristics of the echoing object, the output resulting from angular rotation is then given by

$$F_1^2(\theta, f, \omega) AF_2(d)$$

where ω is the angular rate of rotation.

The amplitude constant "A" is a simplification. It is in general dependent on the frequency, as the reflecting characteristic of an object is almost always frequency dependent.

3.1.2. Forward Motion

Forward motion produces Doppler Shift in the received signal. This changes the audible signal in addition to that which is caused by a change in distance. For example, consider an object at 10 ft which produces an audible note of 3000 c/s moved to 5 ft. The final note will be 1500 c/s. During the intervening period the audible signal depends not only on the distance to the object but also upon the velocity with which the object is moved and the frequency actually being

reflected during the period of movement. This latter is constantly changing. There is thus a complex change in the echo note during forward movement and this can be written as $F_3(v, f, t,)$ i.e. a function of velocity, frequency sweep and time.

If the object is displaced from the direction of forward motion by a distance "S" two additional factors arise. The rate of change of distance is less and the amplitude varies due to the change in the receiver response with angular direction. The general expression for the echo signal under these conditions is thus

$$AF_2(d) F_3(v, f, t, s,) F_4(d, s, f,)$$

3.1.3. Combined effect

The combined effect of angular rotation and forward motion is thus

$$F_1^2(\theta, f, \omega) AF_2(d) F_3(v, f, t, s) F_4(d, s, f,)$$

The complexity of the echo signal is such that exact analyses requires separate treatment. Nevertheless, following a period of training, the brain is apparently able to interpret this signal when desired, and without a great deal of concentration providing always that there is kinesthetic feedback. Under these circumstances the beam cannot be considered as a single dimension channel but a multiple one, depending upon the "Just Noticeable Differences" in the Doppler changes, and amplitude variations. It should be remembered that the signal/noise ratio is generally high.

It will be noted that a condition of ambiguity arises

in the forward motion. An object off the line of progress may be either to the left or right. Slight angular rotation removes this ambiguity - a simple example of kinesthetic feed back via the wrist.

3.2 The Binaural System

Considering now the binaural system, two dimensions are clearly involved since distance and direction information are contained in echo signals in the two channels. Each channel acts similarly to the monaural system just discussed but with a wider beam. Angular discrimination per channel is therefore poorer but Doppler effects are greater.

In addition to the factors so far considered, there is now directional information involving three parameters - amplitude variation between the two channels, time difference of arrival, and frequency difference. All three can be varied by the design but the first two would normally be made to correspond to natural experience in auditory perception whereby the direction of audible sound is determined. Frequency difference would appear to be a new directional cue.

Time difference of arrival of an echo at the two receptors gives direction uniquely if the backward direction is neglected by virtue of the response of the receptors. Two echo signals introduce ambiguity. This arises because the time of arrival of an echo from one of the reflectors at the left receptor can be compared with the time of arrival of an echo from the other reflector at the right ear say, and vice versa as seen in fig.4. There are therefore four possible objects, two real and two

imaginary. This ambiguity is serious only when the imaginary objects lie within the real co-ordinates of the system, and for this to occur, the real objects which produce the ambiguity must lie within a narrow annulus of the receiving sector. This follows from the fact that the maximum time difference of arrival is of the order of 0.25 ms for an angle of 30° . In other words, the distance to object A from the left receptor must not be more than 3 inches greater or less than the distance to object B from the right receptor.

A similar situation exists for the frequency difference since it is directly related to time of arrival, but whereas time difference is a natural auditory cue, frequency difference is not - so far as has been determined up to the present. Ambiguity in the frequency difference cue therefore produces imaginary objects in the same position as those caused by the time difference cue.

Amplitude difference, introduced by splaying the receptors outwards, reduces the sensitivity of the left receptor to signals from the right and vice versa. This enhances the direction cue for one object. When two are present the two real signals are enhanced if one is to the right and one to the left. One of the ambiguous signals is also enhanced since the strong signal from the left object in the left receptor is compared with the strong signal from the right object in the right receptor. The other ambiguous signal is correspondingly reduced, as now two weak signals are being compared.

Movement of the receptors (or the head) changes the situation. The real objects remain in their true position, that

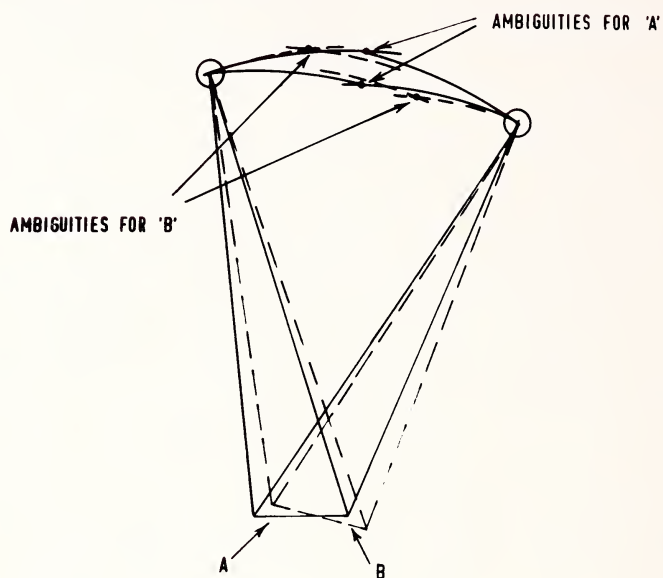


FIG.5 EFFECT OF HEAD MOVEMENTS ON AMBIGUITIES

is they stay still in space, but the ambiguous objects move relative to the real objects as shown in fig.5. Pure rotation has little effect on the ambiguous objects, but the mounting of the receptors on the head is such that pure rotation is virtually impossible and is therefore irrelevant.

Thus it will be appreciated that a very complex pattern of signals is presented to the brain when using this system. Can the brain adapt to it?

4. SUBJECTIVE TESTS

Subjective tests of a very limited nature have been carried out to assess the capability of the man-machine system. Three direction cues were investigated; time difference, frequency difference, and amplitude difference. The latter was not used alone, but was accompanied by either of the former two or both.

4.1 Time Difference of Arrival (T.D.)

In order to have this cue alone a pulsed system was used. Both long and short pulses of tone at a frequency of 50 Kc/s were radiated from an almost point source representing an object at about 6 ft. The source could be moved in an arc of constant distance from the point halfway between the two receivers, and the two receptors were directed ahead. In this way amplitude differences were avoided. The signals in the two receivers were heterodyned with a local oscillator of 47 Kc/s and the subject listened to the 3 Kc/s pulses via headphones which were remote from the fixed receivers. The curved transmitter was disconnected.

An indication of direction was obtained as the radiating source was moved in an arc of $\pm 30^\circ$ about the direction

in which the receivers were pointing. There was a sensation similar to lateralisation, but movement of the apparent source in the head was vague. Variation in the amplitude of the signal following the polar response of the receivers, was more noticeable.

4.2 Time difference plus amplitude difference (TD + AD)

Splaying the receiving transducers a total of 50° greatly increased the direction cue. There was a marked lateralisation effect and the sound in the head appeared to move to and fro as the radiating source was rotated about the receivers.

It was also observed that there was no noticeable change in the amplitude of the signal although there was in fact a marked reduction in the signal intensity for the ahead direction.

4.3 Frequency difference alone (F.D.)

To obtain frequency-difference alone the normal F.M. system was modified. A gate, inserted between the frequency sweep oscillator and the receiver modulators, as shown dotted in fig.1, was closed at the beginning of the sweep for a period in excess of 10 ms. The radiating source was fed from the F.M. transmitting amplifier and, being 6 ft distant, produced an echo note corresponding to 3 ft which commenced approximately 6 ms after the commencement of the frequency sweep. Blanking the modulators for at least 10 ms ensured both audible signals commenced at the same time.

A more distinct indication of direction was obtained than for time difference alone. This was surprising. What was more surprising however, frequency-difference as such was not observed, only what appeared to be normal lateralisation.

Amplitude change was again noticeable, a maximum being observed for on the ahead position.

4.4 Frequency-difference and amplitude difference (FD + AD)

Amplitude variation over an arc of at least 50° disappeared when the receiving transducers were splayed a total of 50° . The direction cue increased but was not noticeably different from that obtained with time difference plus amplitude difference.

An effect which was common to all tests was a rapid "wow" as the source was rotated about the receivers. This was not very noticeable and appears to be due to the rapid phase change in the H.F. signal in one receiver relative to the other. The effect was more noticeable in the pulsed system.

4.5 Time difference and frequency difference (TD + FD)

This represents the F.M. system operating normally without amplitude difference.

Very surprisingly, there was little difference between this and frequency difference alone. A careful check was made to ensure that two different conditions were being observed.

The "wow" was no more noticeable than for frequency difference alone.

4.6 All three in combination (FD + TD + AD)

As would be expected from the foregoing there appeared to be little improvement, if any, over the directional sensation obtained with TD + AD or FD + AD.

The conclusion drawn from these tests was that

amplitude difference was a dominating cue to direction, but quite clearly a fairly exhaustive study is required to elaborate on these preliminary results.

4.7 Multiple radiating sources

Only one radiating source was used for the previous tests. This was unrealistic as there will generally be more than one object present in the field of view. The system would be useless if only one object could be sensed.

Two radiators were then used, and in one instance three, in an attempt to confuse the subject. From the foregoing tests it appeared that amplitude difference was predominant as a direction cue, and so only this parameter was varied in the following tests. Only one subject was used during the tests and, without head movement as a cue, was asked to point to the direction from which the sound appeared to come. The original radiator together with a second at about 4 ft were used at random either singly or together. The directions of the two radiators were varied from 30° to the left to 30° to the right in random steps of about 10° , sometimes both were on the right and at others were on opposite sides of the ahead position.

These tests were carried out with the receiving transducers (a) pointing ahead, (b) splayed approximately 20° and (c) splayed approximately 50° .

The subject was able to determine the number of sources present and their directions reliably in the very limited number of tests only when the receivers were splayed 50° . A splay of 20° was better than no splay.

On the one occasion when a third radiator was introduced without the subject having any prior knowledge that a third may be used, he gave the direction of one radiator and bisected the directions of the other two.

A decision was forced in each case. At no time did the subject feel very confident of his decisions although the degree of confidence was higher when a splay of 50° was used.

At this point it should be said that the subject was the writer, and the experimenters colleagues who were endeavouring to introduce confusion. There is no doubt in the writer's mind that an inexperienced subject would have had difficulty with many of the situations correctly assessed. More than direction cues were being used; although the only information received was via the headphones. It was, for example, sometimes possible to say that there was more than one source present from the tonal quality of the signal without being able to separate the sources in their respective directions. The experiment established two facts. Amplitude difference is a major factor in determining direction, and it is possible to separate two sources and determine their respective directions without head movement.

It was noted that when only one source was present there was a distinct lateralisation effect, but when two sources were present at different distances and a splay of 50° was used the more distant source appeared to be external to the head. Two other subjects confirmed this. When the two sources were at about the same range, the tendency was to think that there was only one present, midway between the two.

It should be remembered that ideal sources were being used and the audible signals were almost pure tones of constant amplitude. This was less so for a splay of 50° than for no splay, owing to the polar response of the receivers varying with the frequency and modulating the amplitude of the signal.

These experiments, while of academic value, bear little relation to reality when using the system in the form of spectacles mounted on the head transmitting from a curved radiator and receiving reflections from objects in an environment which moves relative to the user.

5. SUBJECTIVE RESPONSE TO THE SPECTACLES:

It is almost impossible to describe the subjective response in the real world. Three statements by blind people are perhaps much more significant.

One congenitally blind user responded by saying, "This must be like seeing". He was already familiar with the monaural aid.

A second sensed that a narrow passage which produced a large number of reflections from the sides, was wide enough to be negotiated when using the spectacles, but was too narrow when using the narrow beam monaural aid.

A third stated that the world remained stationary on turning the head.

Natural auditory cues and facial pressures remained even though part of the face and the ears were shielded by the frames.

At the time of writing, only three blind persons have had an opportunity to use the latest design of spectacles, and for only very short periods of the order of 30 minutes.

Five critical sighted observers introduced to the torch and the spectacles for the first time instinctively felt that appreciation of the spectacles was more rapid. This response is rather different from what would have been expected from the laboratory tests using ideal sources, and it is natural to wonder why.

There are three possible explanations and none were taken into account during the tests.

1. Real objects have a character of their own and the signal from most is of a complex structure.
2. Movement of the head - even only slightly - varies the signals noticeably and body motion has a marked effect.
3. The radiation pattern of the transmitting transducer is far from uniform; as the frequency varies the pattern also varies and points of minimum response become points of maximum response. During the frequency sweep therefore the sensitivity in all directions is heavily modulated.

Hence at no time is a pure signal received and the effect seems to produce more a sense of localisation than lateralisation. For example, when proceeding down a corridor lined with doorways, there is a distinct sensation of the doorways passing by external to the head. Objects some distance ahead

appear to be remote from the head and in a number of cases distinctly characteristic objects are sensed approximately in their true position. When there is a clutter of objects covering a wide arc one has a panoramic appreciation of these; individual items are not distinct unless one has, itself, a distinct character. A gap in a clutter of objects is discernable and in certain cases the edges are sharply defined. Little more can be said at this stage; a very exhaustive study is required in order to understand fully the factors involved. Many questions come to mind and they will probably be as difficult to answer as those on natural hearing have been in the past.

DISCUSSION

It cannot be said at this stage that blind people will be able to use the system described; it does however open up a new approach to environmental sensing for the Blind and may lead to a better understanding of the ability of some mammals to use sonic waves in order to sense their environment.

The step which has yet to be taken to produce the true ultrasonic localisation may be technically difficult, but the result is not so difficult to visualize. As explained in the introduction, each object should appear to make characteristic sounds which can be recognised. Since it will be unlikely for two objects to produce exactly the same sound at any one time, the observer should then be able to distinguish one from the other and therefore appreciate their relative positions. In a cluttered environment it is still difficult to accept the possibility of being able to appreciate sufficient detail from

which to reconstruct the spatial pattern. The behaviour of the bat suggests that it can do this using a similar sensing process. It must, for example, require more than simple object detection when catching insects among foliage. Many other examples can be brought to mind. The acuity which the bat enjoys may perhaps be likened to vision where a general overall picture of the environment is obtained at a glance. Fine detail requires examination over a period of time and whereas the eyes can focus attention on a limited area, the ears may focus attention on a particular object or a characteristic sound apparently emanating from that object.

Experience with the ultrasonic spectacles has led to these thoughts, it remains to be seen what a period of learning will produce in the way of pattern transformation.

Abstract

Blind people are generally able to sense their environment by means of audible echoes resulting from clicks, snapping of fingers, etc. Electronic "clickers" have been designed which enhance this ability considerably, but are unacceptable because of the noise they make. The use of ultrasonic waves to overcome this disadvantage and at the same time enhance the information gained from the clickers is proposed, and preliminary results with a binaural F.M. echo-location system are described. It is shown that the arrangement is rich in information, and a narrow beam version (the Sonic Aid) has already proved to be of value to some blind people. The wide angle system in the form of "spectacles" is much more complex however and extensive subjective tests are necessary before it will be possible to predict the value to the Blind. The studies provide an unusual insight into animal sonar systems.

Sonar of the Blind
Sonar Systems
Echo Detection
Animal Sonar

DISCUSSION

by

L. RUSSELL

Dr. Kay's monaural and binaural devices have in common the fact that they explore the surroundings with an ultrasonic wave that is swept over the octave 45 - 90 kilocycles. In this respect the devices are a step ahead of the earlier sawtooth FM aids, which were narrow-band devices and operated at lower frequencies, for exemple in the twenties of kilocycles.

The reflecting characteristics of an object of some complexity change as a function of scan wavelength, and the octave scan makes possible the communication to the listener of a target "signature" - a message containing more information than simply pitch-for-range and amplitude-for-size. Through more subtle characteristics of the output sound, the user can tell walls from bushes, a hedge from a pedestrian, and so on, provided that he is willing to train his hearing and listen with care.

The monaural aid has been given considerable evaluation; yet opinions differ widely as to its usefulness - immediate and potential. The most negative feature of the aid, perhaps, is no fault of the device itself, but is the existence of its well-established competitor the cane, and the systematized schemes of travel based thereon. A blind traveler will have to choose between the torch and cane if he does not wish to carry both, and it seems that the cane must generally win out in the present stage of development of both travel strategies. The reasons for this, in the writer's opinion, are in part the

dependability of the cane in detecting step-downs at normal walking speeds, and in part the difficulty many blind will have in real-time processing of the auditory data presented.

The foregoing opinion results, in the main, from conversations - formal and informal - with people who have played a role in the aid's evaluation. Against a somewhat pessimistic overall background, however, there are several positive attributes of the monaural aid which one ought to note for what they may signify regarding the potential of the binaural aid.

First, a small number of blind travelers have become so skilled with the monaural aid as to assert preference for it over the cane. Second, a substantial number of the blind who have used the device in trials express interest in owning one, although they might still rely mostly on the cane for their travel safety. Finally, the aid does more than simply help one avoid hazards: a user can explore the environment for the pleasure of it - satisfy his curiosity as to the things that line his route as he walks, and so on.

The binaural version, in the writer's view, is an extremely different thing from the monaural. The difference is much more than just the addition of the second channel. The monaural torch is a one-direction-at-a-time probe, whereas the binaural device displays all directions at once, and is an attempt, if you will, to create what would amount to a pseudo-vision of a sonic nature. To give the user an auditory "picture" of the nearby forward surroundings is a possibility that has intrigued many workers in the field, including the writer, and Dr. Kay's binaural aid will re-

present the most technically-refined attempt to do so to date.

Since it is not hand-held, its use will not conflict with that of the cane. If it is not conspicuous in appearance or uncomfortable to wear, its use will not be a burden to the traveler. These may seem peripheral factors in view of the aid's objective, but in the writer's opinion they are important. If the minor nuisance aspects can be minimized, then some travelers can use the aid for weeks or months in their daily journeys without sacrifice of safety or comfort. Then, after a great deal of practise, answers may be found to these basic questions: Can the hearing machinery of the human become matched to the display code of the aid? How long before the sounds are more than a jumble of tones and whistles? In time will the user become adept at making them into pictures or at least rough constructs of the environment? Can the data be processed fast enough? Can its assimilation become a graceful and effortless process? Can the user learn to ignore sounds that require no action, much as he might now ignore the sound of an aircraft overhead? We don't know the answers at the present, but hopefully we shall soon.

What the aid attempts to do - achievement of a sort of instrumented auditory "vision" - is a most ambitious objective. If only a very small fraction of the blind take readily to this technique and get from the aid the benefit that seems potentially there, the project will have most worthwhile.

DISCUSSION

par

L. PIMONOW

Dans de multiples cas chez les personnes normales, l'oreille permet de localiser et de reconnaître l'objet émettant ou réfléchissant des sons. Par exemple, l'approche d'une voiture peut être reconnue aussi bien par l'audition que par la vision.

Le maximum d'informations est fourni dans un tel cas par la variation d'un niveau sonore et par la décomposition spectrale auditive des sons relatifs à l'objet.

En conséquence, il nous semble que le principe du sonar ne doit dans aucun cas, gêner l'audition normale.

Il s'ensuit que toutes les études relatives à la reconnaissance et à la localisation sonore doivent être faites dans un bruit d'ambiance normale, ce qui ne semble pas être le cas des expériences faites par M. KAY et par M. RICE.

Deux autres conditions trop artificielles et s'éloignant des cas pratiques étaient, d'une part les trop courtes distances choisies au cours des expériences, entre les objets et l'observateur et, d'autre part, la limitation du nombre d'objets à détecter.

En effet, le sonar commence à avoir une valeur pratique à partir d'une distance qui nettement dépasse la possibilité de la détection tactile, c'est-à-dire à partir d'une distance dépassant 2 à 3 mètres.

Or, les difficultés essentielles apparaissent précisément quand la distance et le nombre des objets augmentent.

On peut presque dire que dans le cas du sonar pour aveugle, on doit commencer par le problème de la reconnaissance des formes, l'établissement de la quantité d'informations nécessaires et ensuite rechercher les conditions acoustiques appropriées.

Sans entrer plus profondément dans la discussion de ce problème on peut prévoir avec une grande probabilité, que les informations acoustiques seront insuffisantes pour la détection des agglomérations comportant un grand nombre d'objets.

Même au cours de la détection acoustique, des objets quasi isolés comme le font les animaux, il est très probable qu'une certaine quantité d'informations est fournie par d'autres moyens de transmission et, qu'en plus, une grande quantité d'informations devrait être stockée préalablement dans la mémoire de la bête.

En revenant au détail des expériences faites par M. KAY et notamment sur le point de la localisation d'objet par l'effet stéréophonique, rappelons que cet effet consiste en la perception des intervalles de temps (des déphasages) de quelques dizaines de microsecondes dues aux distances différentes de parcours des sons.

Or, la très petite différence de temps de parcours peut être très facilement perturbée par une variation aléatoire des coordonnées du système, comme par exemple par un tourbillon d'air. Les expériences faites, il y a plusieurs années au CNET et relatives au téléphone U.S. l'ont démontré. L'utilisation de cet effet temporel sous forme de variation de la tonalité et que propose M. KAY semble être d'un intérêt relatif.

En outre, comme nous l'avons dit, la perception du spectre constitue une propriété très importante pour la reconnaissance d'objets. Les tonalités comme aussi bien tous les phénomènes physiques qui portent des informations relatives aux autres phénomènes physiques, doivent être considérés comme des éléments d'un code. Par exemple, le bruit croissant produit par une voiture qui s'approche présente un signal en code sonore qui transmet le déplacement d'un objet.

Le même déplacement peut être aussi transmis par le code des rayons lumineux. L'interprétation de ces codes exige un conditionnement acquis par les êtres vivants sur le chemin de l'apprentissage et plus rarement sur le chemin inné.

Or, la localisation angulaire d'objets proposée par M. KAY, par une différence de tonalités relative à la perception binaurale présente une nouvelle interprétation du spectre, c'est-à-dire l'introduction d'un nouveau code exigeant un conditionnement complexe et composé d'éléments qui ont déjà acquis, sur le chemin.

de l'apprentissage, d'autres significations.

Il est donc à craindre que ce double emploi des données spectrales peut conduire à des perturbations de la reconnaissance des objets par le spectre sonore.

Cette crainte s'accroît si l'on admet que l'utilisation du principe du sonar technique ne doit pas exclure l'utilisation quasi simultanée de tous les avantages que présente l'audition normale.

Par contre, la détermination de la distance dans le système monaural, présentant un conditionnement relativement simple et n'étant pas fonction de très petits intervalles de temps de parcours qui peuvent être perturbés, doit être, à notre avis, retenue.

De même le remplacement des sons par des ultra-sons, proposé par M. KAY doit être considéré comme un avantage évident pour de multiples raisons que nous allons mentionner et en particulier en raison de l'accroissement du pouvoir séparateur qui croît avec la fréquence.

En ce qui concerne les multiples mesures exécutées par M. RICE et qui sont données dans beaucoup de cas sous forme de diagrammes, elles présentent un apport très important dans l'application du sonar chez les aveugles.

Bien que, comme le dit l'auteur lui-même, ces mesures représentent seulement une partie préliminaire du programme, on pourrait déjà exprimer quelques critiques et faire quelques suggestions relatives au développement futur de cette importante étude.

Il est parfaitement exact, comme nous l'avons déjà dit, que l'utilisation des sons aigus, à meilleur pouvoir séparateur, est plus avantageuse pour le sonar. Cette constatation étant confirmée expérimentalement par M. RICE et, que de plus, la transposition électronique des ondes sonores en ultra-sons ou vice versa étant relativement simple, il nous semble que l'utilisation d'ondes courtes, sans tenir compte de l'audiogramme du sujet, peut être admise comme la plus avantageuse et les mesures peuvent être faites exclusivement en tenant compte de telles ondes.

En effet, au cours de la démodulation, on peut choisir le son le plus approprié pour l'audition du sujet et le moins gênant pour la transmission acoustique normale.

Les informations permettant de détecter le genre de la surface de l'objet réfléchissant sont dans la majeure partie fournies par la comparaison du spectre des signaux émis avec celui des signaux réfléchis y compris l'absorption.

Cette comparaison exige que le signal possède, d'une part, un spectre suffisamment riche, et d'autre part, un spectre pouvant être confortablement mesuré par l'analyseur auditif. C'est pour la seconde raison que probablement le spectre, soutenu plus longuement dans le temps et relatif au signal de sifflement, comme le constate M. RICE, est plus avantageux que les spectres plus étendus mais instantanés d'un signal bref.

Dans ce cas, comme aussi bien au cours de mesures ultérieures, il sera souhaitable d'utiliser un plus grand nombre de signaux pour pouvoir s'approcher davantage des conditions optimales. Par exemple, la détection qualitative des surfaces des objets pourra être théoriquement mieux faite, en utilisant des séries de signaux brefs (à spectre continu) ou avec une fraction de bruit blanc, qu'avec des signaux soutenus à spectres étroits et discrets.

A ce propos, les informations relatives à la partie du spectre utilisé par les chauves-souris dans la détection des objets, pourraient servir d'indice important dans les recherches du sonar pour les aveugles. Malheureusement, une certaine absence de collaboration entre les chercheurs de disciplines différentes entrave ce genre de recherches.

En revenant à la détection des surfaces ou des agglomérations de plusieurs objets, nous nous heurtons au problème plus général des relations existant entre la théorie de l'information et le fonctionnement du sonar humain. Par exemple, l'établissement théorique de la quantité d'informations nécessaires pour la détection des objets, ou le problème d'adaptation de l'oreille au débit instantané (de pointe) qui est très supérieur au débit moyen, ainsi que l'introduction de l'influence de la constante de temps physiologique dans

le calcul préliminaire, pourraient sensiblement diminuer le nombre de tests expérimentaux en les orientant vers des solutions tracées par le calcul théorique et en particulier par la théorie de l'information.

C'est le manque de préparation théorique qui, à notre avis complique et alourdit les travaux de M. RICE.

On peut, par exemple, établir le nombre d'informations dont on a besoin pour différencier une aiguille parmi beaucoup d'autres ou une porte dans un mur nu. En estimant la vitesse avec laquelle l'aveugle doit découvrir ces objets, on peut évaluer le débit exigé et le comparer avec le débit des informations que fournit le sonar.

Cette remarque est aussi valable pour le sonar animal.

On devrait évaluer le débit qu'émet la bête et ensuite le débit nécessaire pour détecter la cible.

Si par exemple, le débit des signaux se révélait insuffisant alors on devrait rechercher d'autres sources complémentaires d'informations.

A ce propos et plus généralement à propos des discussions fréquentes à cette réunion et relatives à la quantité d'informations fournies par les signaux isolés émis par les différentes bêtes, je rappellerai que cette quantité est déterminée non pas par un signal unique, mais par l'ensemble des signaux qu'utilise la bête.

Par exemple, la capacité d'une lettre "A" est déterminée tout d'abord par l'ensemble des lettres de l'alphabet. En admettant qu'il existe 32 lettres "phonétiques", on obtient une capacité :

$$n = \log_2 32 = 5 \text{ bits/lettre.}$$

Mais les probabilités d'apparition de chacune de ces lettres n'étant pas les mêmes et qu'en outre, certaines lettres étant en corrélation entre elles, le débit est de ce fait très inférieur. Pour la langue française, il est estimé à

$$n = 3,03 \text{ bits/lettre.}$$

Il s'ensuit que pour discuter de l'importance informationnelle d'un signal sonore émis par une bête on doit tenir compte de toutes les impulsions que la bête utilise, de la probabilité d'utilisation de chacune de ces impulsions et également de la corrélation qui existe entre elles. C'est à dire qu'il s'agit de déterminer quels signaux sont utilisés plus fréquemment que les autres et ensuite de définir leur corrélation entre eux.

Si, par exemple, un signal est souvent suivi au même intervalle par un autre, l'information que porte le deuxième signal est faible et devient zéro si cette suite est permanente (+).

C'est en établissant ainsi, d'une part, le débit informationnel d'une série de signaux de localisation et, d'autre part, le débit nécessaire pour la localisation de la cible, que le bilan informationnel peut être dressé.

Malgré ces objections, les mesures faites par M. RICE sont le résultat d'un excellent et très utile travail qui, à notre avis, doit être poursuivi sans négliger toutefois certains calculs théoriques préliminaires.

Pour terminer, je voudrais attirer l'attention sur une certaine propriété de l'oreille qui pourrait contribuer à la réalisation d'un sonar valable et qui pourrait dériver du sonar de M. KAY.

Comme je l'ai mentionné, il semble que le débit des informations pouvant être transmises par les ondes réfléchies est insuffisant pour la reconnaissance des agglomérations (concentrations) de plusieurs objets; on doit donc rechercher des propriétés particulières d'audition qui permettraient d'augmenter ce débit au moins dans les intervalles de temps quand l'effort de reconnaissance est le plus grand.

Pour pouvoir discuter de ce problème, je rappelle que la capacité informationnelle d'un récepteur est donnée par la relation classique de Hartley:

$$n = \frac{1}{\Delta t} \cdot \log_2 S \text{ bits/s,}$$

(+) Si l'émetteur est mobile, la corrélation dépend également des relations spatiales.

où Δt est la constante de temps du système ou le seuil différentiel de temps.

S est le nombre de seuils différentiels d'amplitude (ou de fréquence).

Or, si l'on transmet une conversation, au cours des intervalles T de silence, le son garde un seuil nouveau, d'où :

$$S = 1 \quad \text{et} \quad n = \frac{1}{\Delta t} \cdot \log_2 \quad l = 0 \text{ bits/Ts.}$$

Il en est de même si l'on prononce longuement (Tsec) un son périodique dont l'amplitude ne varie pas et si le récepteur arrive à intégrer les périodes comme le fait l'oreille. C'est le cas par exemple, des voyelles soutenues trop longuement.

Le son périodique complexe (par exp. les formants) garde alors aussi un seul niveau d'où :

$$S = 1 \quad \text{et} \quad n \rightarrow 0$$

Toutefois, la perception de silence ou de phénomène périodique n'est pas immédiate, mais est fonction des propriétés physiques ou physiologiques du récepteur et en particulier de la constante de temps du système. C'est pour cette raison que l'on a remplacé le signe d'égalité par des flèches qui signifient que le débit n tend (très vite) vers zéro.

Si, par contre, on prononce une consonne explosive comme t, p, k etc... dont la prononciation dure une quinzaine de millisecondes, l'amplitude change dans cet intervalle ($T \ll 15 \text{ ms}$) un grand nombre de niveaux.

Physiquement, le niveau varie continuellement d'où on aurait $S = \infty$, mais de fait dans le cas de l'oreille S est déterminé par le seuil différentiel d'amplitude et de temps auditif.

Si l'on admet que pour pouvoir différencier les consonnes les unes des autres, prononcées non seulement par une personne, mais aussi par des autres personnes, comme par exemple, les fillettes, les hommes, les enfants, etc..., on doit admettre que l'oreille doit pouvoir suivre les variations d'amplitude au cours de 15 ms, au moins une vingtaine de fois, d'où on obtient :

$$S = 20 \text{ int } = 15 \text{ ms}$$

De ce fait, les mesures faites au CNET par le bitmètre auditif ont permis de constater que le seuil différentiel d'amplitude chez les personnes normales est très inférieur à 1 ms.

En introduisant $S = 20$ et $\Delta\tau \approx 0,5$ ms dans l'équation de Hartley, on obtient :

$$n_T = \frac{T}{\Delta\tau} \cdot \log_2 S = \frac{15}{0,5} \cdot \log_2 20 \approx 125 \text{ bt/T,}$$

soit un débit dans une seconde $n \approx 8\,500$ bits/sec.

En conséquence, l'oreille arrive à suivre un nombre de seuils différentiels d'amplitude très supérieur à 20, de sorte que le débit de "pointe" mesuré par le bitmètre donne une valeur de l'ordre de 30 à 80 kbits/s.

La mesure, par le bitmètre, du seuil différentiel de temps est faite de sorte qu'on applique une ou deux impulsions qui se suivent à un bref intervalle. L'intervalle minimal qui permet encore de différencier une ou deux impulsions est considéré comme seuil différentiel de temps.

Etant donné que cet intervalle est souvent inférieur à une milliseconde et que d'autre part, la période réfractaire des influx nerveux qui représentent en quelque sorte des marques de temps, est égale ou supérieure à 1 ms, on doit admettre que la mesure des très brefs intervalles de temps ne peut être faite par l'oreille sur l'axe de temps, mais probablement par l'analyse spectrale.

Toutefois, si on applique non pas deux impulsions mais un plus grand nombre, la sensation se transforme en une perception tonale et le seuil différentiel auditif commence très vite à augmenter, pour se confondre avec la constante de temps Δt "auditif" qu'on estime à quelque 60~70 ms.

En conséquence, le débit optimal peut être perçu par l'oreille non pas continuellement, mais seulement dans de courts intervalles. C'est une remarquable propriété de l'audition qui permet à l'ouïe de s'adapter, si besoin est, aux débits très supérieurs du débit moyen.

En effet, le débit moyen qui est déterminé par la constante $\Delta t = 65$ ms est quelque 100 fois inférieur au débit de pointe.

Cette propriété de l'oreille devrait profiter au sonar et notamment, lorsqu'on s'approche des objets, le débit nécessaire à la reconnaissance croît très sensiblement.

En effet, des calculs élémentaires démontrent que pour localiser un objet par des impulsions avec la même probabilité d'erreur au fur et à mesure de l'approche avec une vitesse constante, la cadence des impulsions doit croître exponentiellement.

Pour reproduire un effet semblable par le sonar, à première vue, on pourrait appliquer un déclenchement des signaux par le signal de retour. Le temps de retour étant de plus en plus bref lorsqu'on s'approche de la cible, la cadence des signaux s'accroît. Malheureusement, quelques expériences de ce genre, faites au Laboratoire du CNET ont démontré que le système ne fonctionne bien que lorsque l'on est en présence d'un seul objet. En effet, les réflexions provoquées par un grand nombre d'objets brouillent le déclenchement.

En outre, pour éviter le déclenchement du signal suivant par le signal de l'envoi, on utilise des signaux ultra-sonores proposés par M. KAY et on déconnecte le microphone dans les intervalles "d'aller" des signaux d'émetteur vers la cible et on le branche pour l'intervalle de "retour". A la réception, le signal U.S a été transformé en signal sonore par une modulation appropriée, comme le propose M. KAY.

Cet effet donne en outre l'impression que les objets deviennent des sources sonores.

Malheureusement, ce principe, tout en compliquant le système de M. KAY ne résout pas le problème de la détection d'un grand nombre d'objets qui simultanément réfléchissent les U.S.

En conséquence et avant qu'une possibilité d'adaptation du débit aux circonstances soit trouvée, l'appareil de M. KAY représente d'ores et déjà une solution valable dans la réalisation des sonars pour les aveugles, aussi bien du point de vue technique que du point de vue d'application d'une conception nouvelle, et mérite une vive félicitation.

DISCUSSION

by

J. A. LEONARD

In the case of both these papers, there are a number of small points of fact which have been settled in private discussion with Dr. Rice and Professor Kay. I therefore want to use my time by showing in a more general way where these two papers fit into the field of study of blind mobility, and to make one remark each concerning the two main papers.

In the first instance, when discussing blind mobility, we do make a distinction between problems of orientation or navigation and problems of obstacle detection. Until quite recently the accent has been more on obstacle detection, and both the main contributors to this session have made important contributions to our understanding here. Secondly, it is useful to consider blind mobility situations as entries in a two-by-two table:

Unfamiliar	Familiar		
Lamp-post	Corner of Table	Regular	} occurring obstacles
Bicycle	Child's Toy	Randomly	

We can think of either a familiar or an unfamiliar environment, and within these, of obstacles occurring regularly or randomly. Clearly the most difficult situation is that represented in the bottom left-hand corner, with randomly occurring obstacles in an unfamiliar environment. Diagonally opposite is the situation in which the 'obstacle' turns into a useful landmark, to be avoided or encountered as the case demands. Even in an unfamiliar area a regularly occurring obstacle like a series of lamp-posts may be regarded as a reassuring landmark.

Thirdly, it is possible to present a table of resources and requirements for blind mobility such as the one presented here (see table I). There are two points I would like to make

with the aid of this table: to the totally blind, or even to those with very small amounts of residual vision, hearing is of tremendous importance as the only remaining reliable distance receptor. It is used not merely for communication, but also as an all important instrument for both orientation and obstacle detection. (Note that it is not very useful for objects below the level of the knees). At the same time, human hearing for these purposes is not particularly efficient. Our mechanisms of hearing, so sensitive and acute when we deal with language or music, are poor for handling objects in space.

I hope that this brief statement may help to show the tremendous importance and relevance of the work of both Dr. Rice and Dr. Kay. On the one hand it is essential for us to know what can be done with the unaided ear, and what can be done to train it for better use. On the other hand, and given the potential richness of auditory perception it is right that efforts should be directed towards utilising it to enable blind people to handle objects in space in a more efficient manner. Indeed, it is only by combining the knowledge obtained in both these areas of research that we can hope to arrive at solutions which are not only scientifically interesting but also useful.

I now want to turn to a point raised by Dr. Rice when he cites Griffin's challenge on p. 4 of his paper. Griffin drew the comparison between animal's ability and that of man in using echolocation and stressed the need for basic research on human abilities rather than on human engineering. I agree with this whole heartedly, but have two reservations. I am sure that Griffin would agree to a procedure in which natural observation would at least go hand in hand with, but possibly precede, careful laboratory study. I am also convinced that in this area of research it is at the very least questionable whether one is justified in a programme of research which is totally divorced from application. In stead, I would suggest that one should follow the precedent set by Ivo Kohler whose contribution to this particular topic was undoubtedly enriched by the fact that he set out to teach blind people to make use of the knowledge he had acquired by laboratory studies. In

any experiment with blind subjects one is almost bound to put one's subjects in a situation which enhances and emphasises their impairment. I believe that one is only justified in doing this if one is also prepared to take steps to reduce the impairment effectively.

It will be easily seen that my personal reactions to Griffin's challenge are complementary scientifically, quite apart from any ethical considerations. For it is surely only through the constant interplay between laboratory and field work that one can hope to arrive at some sort of understanding.

Turning now to Professor Kay's paper, I must begin by a tribute to a very considerable contribution on both the theoretical and applied sides. His work on blind aids has already had a tremendous impact on the whole area of blind mobility and I am sure that it will continue to have the same impact. Those of us who have been associated with him during these last few years know of the great difficulties he has had to overcome and the trials he has had to contend with. I suppose it would be no exaggeration to say that I was at least one of these trials. Those interested in an account of the first phase of our collaboration will find it in Leonard and Carpenter, 1964, which contains pictures of the slides shown.

Earlier on, I tried to show the absolute necessity for a blind man to have information in detail about the environment around him, and to obtain this information at some distance from relevant objects. There is no doubt in my mind that Professor Kay's devices are by far the best we have yet seen on the information gathering side, and possibly also on the processing side. The difficulty arises when this information has to be displayed to the user - and all our arguments over the last four years have hinged around this. For once it had been accepted that any active energy device was unlikely to be of reliable use for the detection of low obstacles or holes in the ground, and once emphasis shifted from obstacle detection to environment sensing there still remained this hard core of difficulty. This is best exemplified by the fact that, while there are now people who move about with the monaural device by itself, none of them move about with speeds com-

parable to those obtained by cane or dog travellers. My own view is that even for environment sensing we need a form of display which can be attended to at very low levels of consciousness while cruising about, but which can come to life, so to speak, as soon as an alarm is sounded.

From my point of view it is at this point that the two areas of research we have just heard about begin to converge. For if we could find displays of the more natural kind used by Dr. Rice, I am at least hopeful that Professor Kay's system of environment sensing would become positively useful to a very much broader range of blind people.

References

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TABLE I—RESOURCES

REQUIREMENTS	PERSON (i)				AIDS							
					PROVED (ii)				EXPERIMENTAL (iii)			
(a) Attitude Motivation Standards Body Schema Sense of Space	Memory	Residual Vision	Touch	Hearing	Short Cane	Long Cane	Dog Guide	Human Guide	Narrow Beam	Radio Compass	Watch	Map
(b) Near Perception		+	+	+	+	+	+	+	+			
Distant		+	-	+	-	-	+	+	+			
(c) Head Obstacle		+	+	+	-	-	+	+	?			
Body Detection		+	+	+	+	+	+	+	+			
Feet		+	+	-	-	+	+	+	+			
Street Crossing	-	+	-	+	-	-	+	+	-	-	-	-
(d) NAVIGATION												
Routes	+	-	-	-	-	-	+	+	-	-	-	+
Landmarks		+	+	+	+	+	+	+	+	-	-	-
Slope		+	+	-	-	-	?	+	-			
Veer		+	?	?	-	-	?	+	+	+		
Curvature		+	?	-	-	-	?	+	?	+		-
Texture		+	+	?	?	?	?	+	?	-	-	-
Time	-	-	-	-	-	-	-	-	-	-	+	-
Distance	-	-	-	-	-	-	-	-	-	-	-	+
S		+	+	+	+	+	+	+	+			
Speed M		+	-	?	?	+	+	+	-			
F		+	-	?	-	+	+	+	-			



VII

Contenu social de certaines impulsions
autres que celles utilisées
dans l'écholocation animale

Social communication content
in the pulse outside the echolocation



THE TRANSMISSION OF ARBITRARY ENVIRONMENTAL INFORMATION BETWEEN BOTTLENOSE DOLPHINS

by
Jarvis BASTIAN

Introduction

Sensory communication between individuals is an integral part of any social mode of adaptation, for, at bottom, social behavior and social communication are identical. However, for most social fauna there are episodes of social interaction in which the actions of the participants are sufficiently regular and specialized to justify distinguishing them from other social behaviors as constituting signalling systems. The signalling systems of all vertebrates which have so far been studied, while providing for the communication of certain environmental information, e.g., presence of predators, are very much restricted in their referential ranges because signal emission is keyed to the arousal of emotional states by these environmental events. That is, the signals refer directly to the arousal state of the emitters and only indirectly to the environmental events which evoke such states. In marked contrast, the referential ranges of man's linguistic signalling systems are not restricted to matters of emotional significance (1, 2).

The signalling system of the Atlantic bottlenose dolphin (*Tursiops truncatus* Montagu) has been suggested as another possible exception to this limitation on the grounds of their extensive exploitation of acoustical signalling in their social interactions, the ready susceptibility of their phonatory emissions to experimental control, and the notable specialization of their nervous systems (6, 7, 9). The research reported here was designed to test

The research reported here was conducted at the Marine Biology Facility, Naval Missile Center, Point Mugu, California under contracts with the U.S. Naval Ordnance Test Station, China Lake, California, W.B. McLean, Technical Director. I wish also to acknowledge and thank the other people who contributed to its planning (T. Bever and F.S. Cooper), execution (C.L. Anderson, R. Bailey, C. Bowers, R. McClung, and W. Powell), and analysis (C. Wall).

this possibility; to see if the signalling system of these animals was capable of transmitting information referring to arbitrary features of their environment. Unfortunately, because of the obvious difficulties encountered in attempting prolonged and detailed observation of these animals in their natural habitat, very little is known of the specific features of this signalling system, nor what contribution these features make to the overall adaptation of these animals in their free ranging condition. For these reasons, a test of this kind had to be conducted with captive animals and against a background of very little relevant information, forcing the design of the test to be subject to logical and training considerations alone.

The overall objective of the design was simplicity in both the logical and behavioral requirements of the test. The test itself consisted of presenting a pair of these animals, each in a separate compartment, with a task requiring a minimal degree of their cooperation, i.e., simply coordinating their actions. Also for the sake of simplicity, there were only two alternative actions required of each animal, consisting of simply pressing one of a pair of paddles in its enclosure. Which of its paddles was to be pressed on any given occasion was indicated by two alternative states of a light signal. However, this light was presented to only one member of the pair, so that unless it acted to transmit information about the state of the light to the other animal, their performance in the task would remain at the level of chance. But performance in this task would provide a satisfactory test of

the pair's capacity to intercommunicate this information only if certain additional information were available to them, namely that the member of the pair receiving the light signal be aware of the absence of the light in the other member's compartment and of the occasions when the information carried by the light was needed by the other. In order to restrict the test to the transmissibility of information concerning only the state of the indicator light, it was decided to provide the animals with this supplemental information through additional features of the test situation itself and the animals' history of training within it.

Training Procedures

Though the logic of this design was quite simple, a rather intricate program of training was necessary for its effective implementation. The major features of the training program were as follows:

- 1) Preliminary training: The two animals participating in this test were a male and female who were estimated to be 4 and 3 years old respectively at the start of this training. They had been captured about a year before, during which time they had been independently trained to accept dead fish by hand. In the first stages of the program they were separately trained to receive thawed smelt from an automatic feeding device whose activation followed a brief burst of tone delivered 4 seconds before. The frequency of these tone bursts, or "bridge" stimuli, was different for each animal. After becoming well accustomed to approach the

feeder upon presentation of its bridge, each animal was trained to press a submerged paddle located on the opposite side of the tank. Pressing the paddle activated the bridge - feeder sequence. This training continued until each animal was pressing for at least half of its daily ration of 4.5-5.9 kg. of smelt. The animals were maintained on this ration throughout all phases of training and testing, aside from several prolonged interruptions in the training program. Only small adjustments within this range were required to sustain training, even when, in later phases, their whole ration was dispensed in the training situation.

2) Time In Training. In the next stage of training, again with each animal separately, paddle pressing activated the bridge-feeder sequence only when an automobile head-lamp, centered 46 cm. above water-level directly aside the paddle shaft, was shining. Paddle presses occurring when this Time In light was off, that is, Time Out periods, resulted in delaying the next Time In period, when the light would next come on and paddle pressing would again result in the bridge-feeder sequence.

The durations of the Time In and Time Out periods were gradually changed until essentially all paddle presses were confined to a 10 second Time In period even with Time Out periods ranging up to 5 minutes. This degree of stimulus control over paddle pressing was established quite readily (7 training sessions, no more than one per day, for each animal) but only at night, evidently because daylight conditions did not provide sufficient

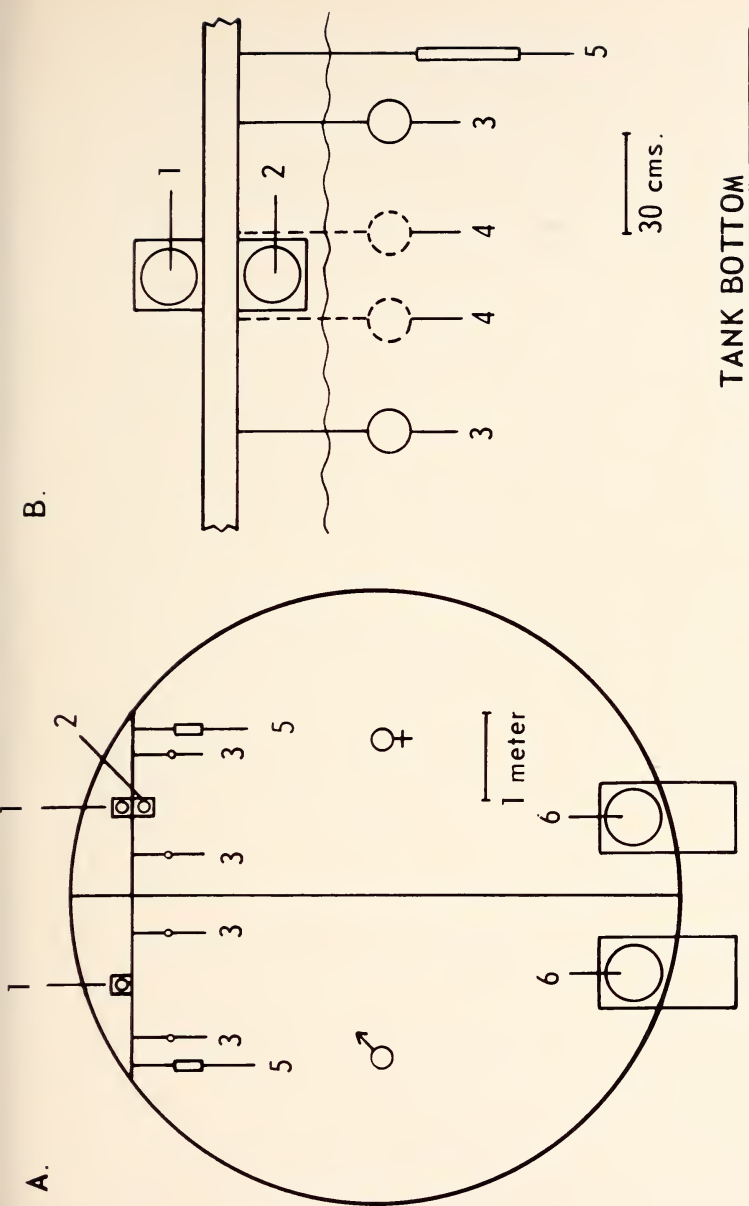


Figure 1: A, Overhead view of training tank; B, side view of

arrangement of lights and paddles on female side. (1) Time

In lights; (2) S^D light; (3) paddles, wide position; (4) pad-

dles, close position; (5) hydrophones; (6) feeding devices.

contrast for the Time In light in the open training tank.

3) Differential Stimulus Training. At the start of the next stage in the program, the animals were again trained separately, though they had free access to each other except during the actual training sessions when they were separated by a net drawn across the diameter of the tank. Later they were transferred to another tank whose top and sides were enclosed by a canvas covering in order to provide sufficient darkness within the tank to permit training during daylight. In this tank a net permanently separated the animals for the remainder of the investigation (see Fig. 1-A). During this stage of training, each animal was presented with 2 paddles, but only one at a time at first, whose positions were separated by 1.07 meters, center-to-center, with the Time In light placed between them at the same level above the water line as before. At first, 2 additional lights were introduced, one aside each paddle shaft at a level some 20.3 cm. below that of the Time In light. At the start of a Time In period one of these additional lights would come on simultaneously with the Time In light. The light alongside the paddle to the left of the Time In light shone intermittently, with a 1/sec. interruption rate, while the light alongside the paddle to the right shone continuously, when on.

Initially, only one paddle and its adjacent light were presented during a Time In period, and the conditions were the same as during the preceding stage of training. Later, both paddles were in position at the same time but only the paddle whose light

was on would activate the animal's bridge-feeder sequence, followed 2 seconds later by the offset of that light together with the Time In light. A press on the other paddle resulted in an immediate Time Out. Then, the positions of the lights associated with each paddle were gradually shifted towards the center until they were aside each other directly beneath the Time In light. At this point, one was eliminated, leaving just one light, the discriminative stimulus, or S^D light, which could be activated in either the flashing or steady mode. In all the remaining training and testing, the mode of S^D light operation was determined by a random schedule, except that when the animals committed an error the same S^D condition prevailed in the subsequent Time In period.

This phase of training required a total of 21 and 18 sessions for the male and female respectively to reach a performance level of 90% correct, though establishment of the differential control of the paddle pressing proceeded much more rapidly when the training was transferred to the covered tank. Upon reaching this level of performance the animals were each given 3 additional training sessions.

4) Coordination and Dependency Training. Up to this point, the animals had been trained individually. In leading into the next phase of training two sessions were conducted with both animals concurrently, though independently. Following this, one session was run in which the onsets of the Time In and S^D lights for both animals coincided. Then a further restriction in the training

conditions was introduced in which the male was required to press the appropriate paddle on his side of the tank before the female pressed hers. The Time In and S^D lights for both animals went on simultaneously, with the S^D mode the same for both. If the male pressed first, his bridge was presented immediately and this, together with the sound produced by his paddle press, signalled the occasion for the female to respond. If she was also correct, her bridge was sounded and then, and only then, the feeders for both animals were activated. An incorrect response by either animal, including the female's pressing before the male, resulted in an immediate Time Out for both animals. Later, time restrictions were also introduced which required both animals to perform correctly within these limits; failure to meet these restrictions by either animal resulted in Time Out for both.

The next step in training involved gradually introducing a delay of 5 sec. between onset of the Time In light and onset of the S^D light and at the same time reducing the length of time during which the male could respond correctly. These changes were made to induce the male to respond to the Time In light as an "alerting" signal separate from the S^D light. To further promote this dissociation of the male's Time In and S^D lights and set the stage for the next phase of training, his Time In light was gradually moved towards the female's side of the tank until it was finally adjacent to her Time In light, at which time one light was removed. By this time each animal had also been trained to perform its

respective paddle presses within a 5 sec. interval set for each.

In the next phase of training, the location of the male's S^D light was also gradually shifted towards the female's S^D light, until it was close enough to be removed. At this point the male was entirely dependent on the female's array of lights for both Time In and S^D signals; the onset of the single Time In light would be followed 5 sec. later by the onset of the single S^D light, following which the male had 5 sec. in which to respond successfully, in which event the female then had 5 sec. to do likewise. A 30 sec. Time Out separated a successful performance from the next Time In signal. After this point had been reached the single Time In light was then moved gradually until it was finally in the original position on the male's side. Several sessions later the female's Time In light was reintroduced into its original position, resulting in the final configuration of the various light signals portrayed in Figure 1.

The incorporation of all these restrictions into the animals' performances proceeded by bringing the joint level of performance success to 90% at any one stage of training before introducing the next. Twenty-nine sessions, with approximately 300 Time In periods in each were needed to reach this final stage of training. Then, in order to stabilize the performance and protect it against some of the difficulties that were to be expected in the subsequent testing, 4 additional sessions were conducted during which the animals were accustomed to receiving fish only after correct performances on up to

5 Time In periods, though on the average every other successful performance was rewarded, and all correct paddle presses were accompanied by the animal's bridges.

Testing Procedures and Results

A canvas curtain was installed within the tank enclosure so that it could be drawn to form a visual barrier between the male and female sides of the tank. Its height reached from the overhead covering to the tank bottom and it was wide enough so that, when extended, it reached across the diameter of the tank and beyond to the encircling side curtains. During 8 sessions this curtain was drawn by progressive stages from between the two feeding devices to within .91 m. of the cross-support bearing the animals' lights and paddles. Throughout this and all the testing procedures the delay between onsets of Time In and S^D lights was set at 5 sec. with 10 sec. provided for each animal's correct paddle presses and with 20 sec. Time Out between successful Time In periods. In the course of carrying out these procedures the female became increasingly reluctant to eat and finally refused altogether, evidently due to an infection which, though responding rather quickly to antibiotic treatments, reduced the rate at which the pair accommodated the increasing visual isolation. Four additional daily sessions were then conducted with the curtain .91 m. from the cross-support and with varying ratios of correct performances to rewards, during which the pairs' proficiency was consistently above the 90%

level of success. No timing errors were committed during these days and only the male made incorrect paddle presses.

On the next day, after running 184 additional Time In periods on a varying reward ratio (93% successful, no errors by the female), the curtain was drawn to first 40.6 cm. and then 15.2 cm. from the cross-support (7 errors, all male, out of 121 Time In periods with all correct performances rewarded). Then the curtain was drawn all the way to the cross-support, and for the first time the animals were run through the entire contents of the feeder's magazines (57 Time In periods) without committing an error.

On the next day a series of 210 Time In periods was run over which the animals achieved a 97% success level. During this period the curtain was extended from the cross-support to the tank side and beyond to the side curtain of the tank covering and all detectable gaps in the visual barrier between the animals were filled. Various other changes were also made to eliminate possible acoustic cues that might have arisen from the female's S^D light, e.g., lowering the water level so that the S^D light was never in contact with the water and inserting acoustical insulation between the light and its housing.

On the next day of testing, another S^D light was installed on the cross-support. This light was arranged so that it was activated at the same time as the other S^D light, but always in the flashing mode. However, the face of this light was completely masked, so

that if the male had been responding to differential acoustical cues emitted by the S^D light, this additional light would be a source of confusing cues. The performance level was not affected by this condition (97% success level over 59 Time In periods). During the remainder of the day, this "dummy" S^D light remained in operation, and the female's actual S^D light was masked to varying degrees. With the S^D light partially masked ($1/4$ to $3/4$ exposed) the level of performance obtained over 79 Time In periods was 86% correct. With the S^D light completely masked the level of performance over 87 Time In periods fell to 39% correct. As only 2 of the 53 errors in this series were committed by the female, it was apparent that she was able to key her own response to the different acoustic events associated with the male's correct paddle presses when her S^D light was eliminated. Following this series with the S^D light masked out completely, a recovery series of 187 Time In periods was run with 97% successful performances.

These tests appeared to eliminate any obvious artifactual basis for the pairs' successful performance, and further disclosed that their success was contingent on the female's reception of the S^D light signals and on the male's reception of acoustical signals linked, somehow, with the S^D light signals. The possible sources of acoustical cues to which the male could respond are as follows:

1. Apparatus cues. The equipment used in controlling and recording the experimental conditions might have produced differential cues discriminable by the male.

2. "Passive" female position cues. The time restrictions of the task were such that the female's approach to her paddles usually coincided with the male's and might have provided a source of differential cues for him either through the acoustical shadows she might have cast in his acoustical field or through his active echo ranging on her position.

3. Cues arising from phonatory actions of female. The female might have been emitting signals differentially associated with the S^D light signals which is, of course, the possibility this research was designed to test. Although the acoustical events within the tank had been routinely monitored, and a great deal of phonatory activity had been observed, the monitoring system did not permit the identification of the individual animals, nor the analysis of the acoustical events recorded.

The determination of which of these possibilities, singly, or in combination, was responsible for the pair's performance success required an additional series of tests in which adequate acoustical controls and recordings could be obtained. To this end, 8 additional days of training were conducted in which the animals were habituated to the introduction of the required control procedures.

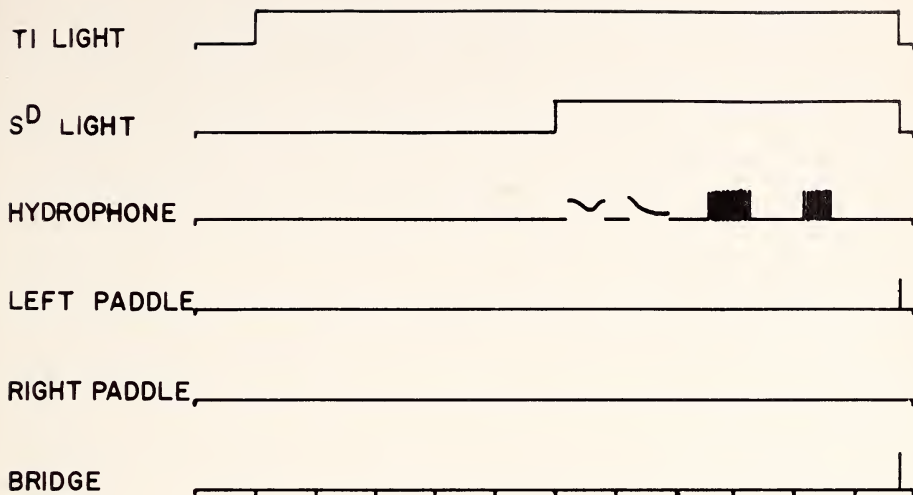
Acoustical Test Procedures and Results

There were 3 additional control procedures incorporated in the tests run with adequate acoustical recordings. These were: 1) a more elaborate "dummy" S^D light unit, again fully masked, but independently programmed to operate in a mode exactly parallel though

opposite the actual S^D light; 2) reducing the inner edge distance between the female's left-and-right paddles from .91 m. to less than 15.2 cm. and turning off the filter pump located on the female's side of the tank which was an important noise source in the tank; 3) an acoustical barrier composed of Neoprene sponge sheeting (the material used in the construction of diver's "wet suits") attached to 3 panels of plyboard which, when all were positioned along the length of the dividing net provided a high level of acoustical separation between the two sides of the tank. This acoustical insulation served not only to reduce the amplitude level of the animal's sound emissions across it but thereby increased the separation in the recording of each animal's emissions.

On two consecutive days these additional control procedures were systematically introduced, alone and in combination, and the animal's sound productions were recorded. The principal recordings were made through two hydrophones suspended from the cross-support in the positions indicated in Figure 1. Other acoustical transducers were strapped to the two Time In lights, the S^D light and to the main relay racks containing the programming equipment, which was located in a trailer some 20 m. from the tank. These signals were recorded on a multichannel instrumentation recorder with associated components to provide a total system with essentially flat record and playback frequency-response characteristics to beyond 300 kHz for the 2 principal hydrophone channels. The recordings from these two channels were then dubbed with an 8 fold

FEMALE



MALE

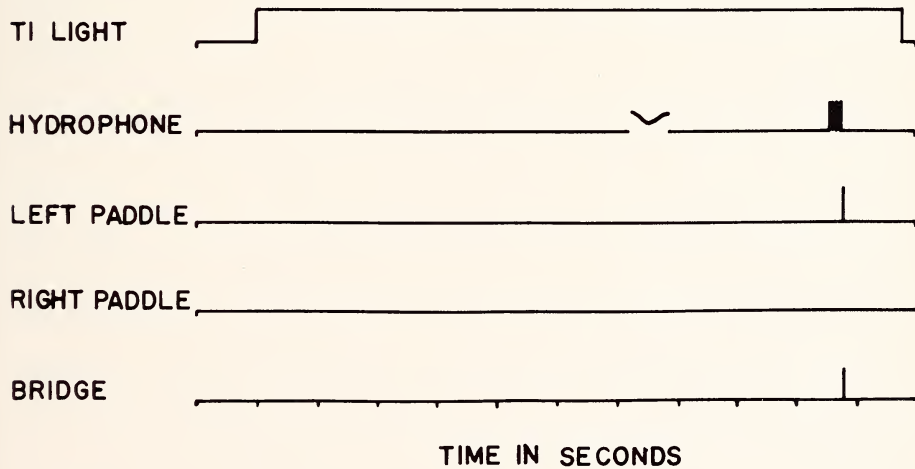


Figure 2: Typical sequence of control signals, acoustic events,
and paddle responses occurring within a Time In period.

time expansion.

These dubbings, totaling more than 20 km. of tape, were then edited to collect the recordings of all the flashing and steady Time In periods for a given run on separate reels and to identify and mark the onsets of the Time In and S^D signals. Then the edited recordings were transcribed by an oscillograph to provide visual recordings of the acoustical events at a writing speed of 20.3 cm/sec. real time. In addition to the straight oscillographic records, frequency meters were also used to provide synchronized visual displays of the frequency contours of the whistles each animal emitted. These oscillographic recordings thus permitted the reconstruction and analysis of the events occurring within each Time In period in the manner indicated in Fig. 2.

The various conditions and the resulting performances in each of these test runs were as follows:

Run I. The first of these tests was run with only the visual barrier imposed. No acoustical recordings were made. There were no errors over the 30 Time In periods in this run.

Run II. In this run the completely masked "dummy" S^D light unit was installed. The animal's performances on this and all other runs are summarized in Table 1. As the central issue in these tests was the animals' performance in pressing the correct paddles, the analyses of individual performances do not reflect errors in the timing of the animals' paddle presses. Therefore, individual performance levels are expressed in terms of the per cent of

opportunities to respond correctly. The table also presents the relative frequency of S^D periods, i.e., the critical intervals between the onset of the S^D light and the male's response, in which the female emitted whistles and pulses. These results indicate clearly that performances were not adversely affected by the introduction of this source of potentially confusing acoustical stimuli. It should be noted that with but one exception the female emitted both whistles and pulses in every S^D period.

Run III. In this run the distance between the female's paddles was closed which, if the male had been somehow responding to differences in the female's position as she approached the paddles, would have presumably reduced the discriminability of these differences. However, this test proved abortive because the female's feeding device was inadvertently disengaged, effectively putting her on an extinction schedule. This condition was not discovered until the run had been completed as the marked deterioration in performance was first attributed to the change in the female's paddle positions. This deterioration was as much evident in the female's performance as the male's, and the number of S^D periods in which she produced whistles and pulses was markedly reduced.

Run IV. In order to recover the high level of prior performance, especially the female's, the next run was conducted with only the visual barrier in position. The results indicate that the recovery was complete by the end of that run.

Run V. This run repeated the conditions of the earlier Run III, but this time with the female's feeder operating. The results indicate

that there was no appreciable change in performance levels associated with the change in the female's paddle positions. In the last half of this run, the "dummy" S^D light was also reintroduced and the tank's water filter turned off. As the pair's performance was errorless throughout, these controls were eliminated from the remainder of the test runs.

Run VI. In this run the first panel of the Neoprene covered plywood was inserted in position along the dividing net so that it extended out from the tank side between the two light and paddle arrays to some 1½ m. beyond cross-support. An 46 cm. flap of the Neoprene sheeting was stapled to the side of the tank to provide a more complete seal at that juncture. The results obtained with this first part of the acoustic barrier in place indicate that this interfered with performance to some degree. The slight reduction in performance level cannot be entirely attributed to the unaccustomed presence of a novel element in the test-situation. In the preparations for the present tests the animals had been run through several hundred Time In periods under these conditions with closely similar levels of performance; 342 correct out of 405 Time In periods (84%).

Run VII. In addition to the first part of the acoustic barrier, this run was conducted with the female's paddles in their close position. The results indicate that the addition of this condition did not adversely affect the animal's performances.

Run VIII; S^D Exposed. In this run the female's paddles were returned to their wide position, the first panel of the acoustic barrier remained in place, and the face of the female's S^D light was progressively masked, by thirds, until the masking was complete, after which a recovery run was conducted with the light completely exposed. The results obtained with 2/3, 1/3 and none of the light masked were treated together. These results indicate that performance was maintained at high levels of success under these conditions.

Run VIII; S^D Masked Completely. When the female's light was totally masked, the results indicate the disastrous consequences for the animals' performances. But just as in the earlier runs with the S^D light blacked out the joint performance levels did not fall to the 25% expected if the animals had been independently performing at chance levels, because the female was herself performing considerably above chance expectations. Presumably, the female's ability to discriminate the acoustical events associated with the male's correct responses was again responsible for this. It is also of interest to note that there was only one error due to the timing of the animals' responses, indicating some basis for discriminating the boundaries of the critical intervals other than the S^D light itself. As the animals had been run for well over 2,000 Time In periods with the same 5 sec. delay between the onsets of the two Time In lights and the S^D light, this extended experience might have enabled them to time their responses by the onsets of the Time In lights in the absence of the female's S^D light. This point will

be raised later in the discussion of the animal's whistle emissions.

Run IX. This run was conducted with a second panel of the Neoprene sheeting in place so that the barrier extended approximately two-thirds across the diameter of the tank. The flap of the second panel was overlapped and stapled to the first to provide continuity of the sponge sheeting. The female's paddles were in their wide position. The results obtained from this run indicate that this increase in the extent of the acoustic barrier did not materially impair performance beyond the levels obtained with just the first panel.

Run X. The conditions during this run were the same as the previous run except that the female's paddles were changed to their close position. The results indicate substantially the same performance levels as were obtained from the preceding run.

Run XI. In this run the third panel was placed in position and its flaps stapled to the second panel on one end and to the side of the tank at the other end to form a continuous barrier of the Neoprene material between the two sides of the tank. The female's paddles were returned to their wide position. No attempt was made to analyze the properties of the acoustic insulation between the two sides of the tank, but the signals recorded from the two principal hydrophones indicated severe attenuation across the barrier. This was also evidenced by the drop in the male's level of performance; his errors were almost all incorrect presses of the right paddle. There were other notable performance changes associated

with the completion of the acoustic barrier which will be discussed later.

Run XII. The tank conditions during this run remained the same except for the change of the female's paddles to the close position. The overall performance was again depressed. The male's errors were confined almost entirely to one side as before, though in this run the predominant error was his incorrect pressing of the left paddle.

Run XIII. During this run the female's paddles were replaced to their wide positions. A gap in the sponge sheeting was made where it was joined to the side of the tank between the two feeders by loosening the top part of the flap of this material that had been stapled to the tank's side. This flap was folded back and fastened to form a port about 10.2 cm. wide and 50.8 cm. deep between the two halves of the tank. This change had been made to more clearly establish the effect of the complete separation of the two sides of the tank. However, this test proved abortive because of the same mishap occurring in Run III. The female's feeder failed to operate throughout the run, thus subjecting her part of the task to extinction conditions. The results indicate the effect of this unplanned condition on the animal's performance.

Run XIV. The error in equipment operation that occurred during the preceding run was discovered and corrected. The animals were then put through a final run. The obtained results indicate that the previous extinction condition had no adverse effect on the female's paddle pressing performance or on her emission of pulse trains during the S^D periods. The results also indicate that the gap in the acoustical barrier was associated with a return to the prior levels of performance for all aspects of the joint task.

Summary of Test Performance Results

An overall examination of these results indicates that the only experimental conditions which markedly impaired performance were omitting the female's food rewards (Runs III and XIII), masking her S^D light (Run VIII; S^D Masked), and imposing the acoustical barrier between her and the male.

These findings effectively eliminate an "artifactual" basis for the male's performance. If the male had been responding to acoustical cues inadvertently provided by the programming and recording equipment, such cues would have been as much available in Runs III, VIII; S^D masked, and XIII as in the other runs with high performance levels. Neither do the results support the possibility that the male was responding to acoustic differences passively arising from the female's approach to her paddles, for his overall performance on Runs IV, VI, IX, and XI, when the female's paddles were in their wide positions, was 84% correct, but it was also 84% correct on Runs V, VII, X, and XII, when the female's paddles were in their close positions but all other conditions were the same. Furthermore, the male only rarely emitted pulses during the S^D periods, except immediately before striking a paddle when he would characteristically emit a brief pulse train (usually about .15 sec. duration) with an initially high but rapidly falling repetition rate which culminated in his hitting the paddle. This "creaking door" pulse train was also emitted by the female just before her paddle presses and can be confidently considered as part of the animal's paddle pressing action itself and distinct from the vastly

Table 1: Performance and female's phonatory productions by runs

Runs	Condition	Total s ^D Periods	Paddle Errors ^D				% Correct Paddle		% s ^D Per. Female:		No. Timing Errors	Total % Errorless
			Male		Female		Male	Female	Whistles	Pulses		
II	Flashing Steady	13	0	0	0	100	100	100	100	0	97	
		18	1	0	0	94	100	94	100			
III	Flashing Steady	26	10	1	1	62	94	23	27	18	57	
		30	12	1	1	60	94	20	43			
IV	Flashing Steady	14	0	0	0	100	100	86	93	0	94	
		17	2	0	0	88	100	82	100			
V	Flashing Steady	27	0	0	0	100	100	93	96	0	98	
		24	1	0	0	96	100	63	100			
VI	Flashing Steady	19	1	0	0	95	100	79	100	0	86	
		16	4	0	0	75	100	63	100			
VII	Flashing Steady	20	2	0	0	90	100	85	95	0	89	
		24	2	1	1	92	95	83	100			
VIII; s ^D Exposed	Flashing Steady	23	0	0	0	100	100	78	96	0	94	
		25	3	0	0	88	100	76	100			
VIII; s ^D Masked	Flashing Steady	31	19	3	0	39	75	48	90	1	39	
		31	16	0	0	52	100	58	71			
IX	Flashing Steady	18	1	0	0	94	100	100	100	1	94	
		14	1	0	0	93	100	93	100			
X	Flashing Steady	15	1	0	0	93	100	100	100	0	86	
		20	4	0	0	80	100	80	100			
XI	Flashing Steady	29	12	0	0	59	100	100	97	0	68	
		12	1	0	0	92	100	83	100			
XII	Flashing Steady	9	1	0	0	89	100	89	100	3	54	
		26	15	0	0	42	100	96	100			
XIII	Flashing Steady	15	7	0	0	53	100	80	40	5	62	
		11	2	1	1	82	89	73	36			
XIV	Flashing Steady	23	2	0	0	91	100	87	91	1	91	
		24	2	0	0	92	100	92	100			
II - XIV	Flashing Steady	282	56	4	3	80	98	79	87	29	79	
		292	66			77	99	73	89			

different pulse trains emitted earlier in the S^D periods. But although there were no overall differences in the male's performance ascribable to decreasing the distance between the female's paddles, there was an interesting interaction between his level of successes under the different S^D light conditions and the positions of the female's paddles, which will be discussed more appositely below.

The relative absence of pulsing by the male during earlier parts of the S^D periods, before the final "homing" trains just mentioned, indicated that he was not exploiting his echo ranging capabilities to follow the female's position as she approached her paddles. Indeed, if the male had been keying his responses directly to the female's location, there would have been little need for his echo ranging, for Table 1 shows that she was usually a very active acoustic source. She emitted at least one whistle in 76% of the S^D periods and at least one pulse train in 87% of them. In fact, her tendency to emit these sounds closely paralleled the changes in the male's level of success associated with the changes in experimental conditions except when the acoustical barrier was complete (Runs XI, XII). The rank-order correlations between his overall levels of success for all runs, except for XI and XII, and the occurrences of female whistles and pulses respectively were .84 and .56, which strongly suggests a central role for these emissions in the determination of his performance. Her tendency to emit these sounds was especially sensitive to the extinction conditions

of Runs III and XIII. The analysis of these female emissions follows in the next section.

As a final note to this summary of performance results, Table 2 presents the average time elapsing between the onset of the female's S^D light and the male's paddle presses. (These measurements are subject to systematic underestimation. The signals controlling the onsets of both the S^D and Time In lights were recorded through a different channel from those receiving the signals from the hydrophones in the tank. The onset times of these periods was introduced into the audio recordings by superimposing tone bursts onto them as they were being copied from the original. This was done by listening to the channel on which the control events were recorded and activating an oscillator when they were heard, but even though the master recordings were copied with an 8 fold time base expansion, the listener's reaction time resulted in an average delay of approximately 0.1 sec. in the registration of these events.) It is apparent that the male's response times were influenced primarily by the extent of the acoustic barrier between the pair and that on the average his response time was slightly longer when he pressed the incorrect paddle. The difference between his overall response times in correctly pressing his right and his left paddles 3.55 and 3.36 respectively, was not statistically reliable ($t = 1.72$, $p > .10$). However, there were pronounced differences in the way he approached his two paddles. From about halfway through Run VIII through the end of Run XIII (231 Time In periods) an observer was

stationed inside the tank enclosure at the side of the tank just behind the male's paddles. This position permitted him to observe the male's position only when he came within the range of his Time In light, for he remained totally under water throughout nearly all of his approaches to the paddles. These approaches were roughly sketched by the observer, and indicated that in the 148 S^D periods where the male could be seen in Runs VIII, IX, X, and XIII, the male unfaillingly approached the left paddle straight on. This was so even for the 77 occasions in which he went on to press the right paddle. On these occasions he approached the left paddle until his snout was estimated to be within 30 cm. from it, where upon, with a marked increase in speed, he swerved obliquely to hit the right paddle. However, in Runs XI and XII a different approach pattern was observed in 25 of the 74 Time In periods during which these observations could be made in which the male first approached very closely to the middle section of the acoustical barrier, often stopping there briefly, and then proceeded at a comparatively slow speed to the paddles. This different pattern of approach undoubtedly contributed to the marked increase in the male's response times obtained in these runs.

Similar observations were made on the female's paddle approaches during 206 Time In periods starting midway through Run VII and continuing through the end of Run XII. The female exhibited approach patterns that were decidedly different from the male's. There was no evidence of any bias in her approaches to her paddles and in

only 8% of the 186 approaches for which these observations were possible was she observed to approach either paddle in a straight on fashion. Instead, she approached on a line midway between the paddles and then, when quite close to the paddles, would move toward either paddle and hold a position in which her snout was just inches from a paddle with her body either on a line parallel to the cross-support or at a very acute angle to it. Then, when it came time for her response, she would merely make a short sideways swipe at the paddle to which she had been oriented. This same pattern was observed when her paddles were either in their wide or close positions. The only notable elaboration of it occurred in Runs XI and XII when in 19 of the 78 observations she was observed to be making very vigorous vertical bobbing motions with her head while in her "holding" positions alongside a paddle.

Analyses of Sound Emissions

The evidence reviewed above clearly implicates the female's sound emissions as having some connection with the male's level of performance success. To further examine this association, Table 3 presents the contingencies between the male's performance on all recorded S^D periods and the occurrence of at least one female whistle emission during them. The probability of the male's pressing the correct paddle on the condition that the female whistled was .84, but the probability of his being correct on the condition that she had not whistled was .61.

A comparable analysis of the contingencies between the male's performance and the female's production of at least one pulse train for all recorded S^D periods appears in Table 4. The probability of the male being correct on the condition that the female had emitted a pulse train was .83, and the probability that he was correct on the condition that she did not pulse was .52. These analyses provide additional evidence of the association between the female's production of these sounds and the male's performance success.

The occurrences of the two kinds of sounds by the female were also highly associated with each other. Table 5 presents an analysis of the contingencies between their occurrences over all the recorded S^D periods. She was somewhat more likely to emit pulses on condition that she also whistled ($p = .97$) than vice versa ($p = .85$).

The abundant demonstration that these sound emissions were linked with the male's performance success does not, of course, establish these sounds as the basis for his pressing the appropriate paddles. This would require, first of all, a demonstration that the female's productions were different in the two S^D light conditions, and secondly that the male's actions were contingent on such differences in her emissions. Put another way, the female must be shown to effectively encode the information associated with the variable light conditions and the male must be shown to effectively decode this information. Failure at either juncture would drastically weaken any inferences concerning the signalling value of these sounds.

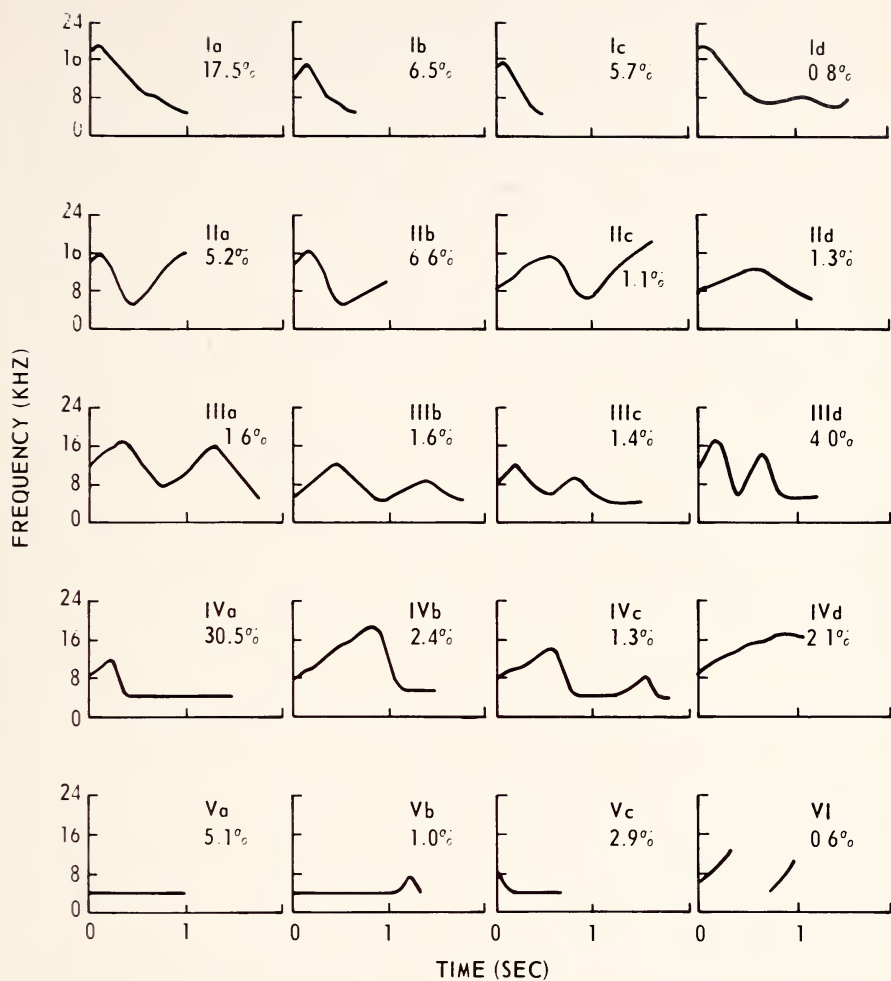


Figure 3: Modal representatives and relative frequencies of each class of whistle contours.

Whistles

To examine the first point, frequency vs. time analyses were performed on the 633 whistles produced by the female and the 413 produced by the male during the 574 recorded S^D periods. These whistle contours were then divided, on the basis of visual similarities, into 20 classes which subsumed all but a miscellany of 0.9% of them. Modal representatives ("type specimens") of each class are presented in Figure 3 together with the relative frequencies with which each classification was made. The most notable feature of the whistles was the marked degree of intergradation between almost all classifications, so that the drawing of boundaries between adjacent classes was largely arbitrary. This is amply attested by Figure 4, which presents the most extreme variants of those whistle contours counted as falling within each class.

It is interesting to note that these whistles represent a very narrow range of the variation in whistle production that has been reported for this species (3). However, the contours observed by Lang and Smith (5) in circumstances much like those reported here, in which a pair of these animals was in acoustical but not visual contact with each other, are easily accommodated by the present classification scheme with their Types A through F falling respectively into classes VI, IVb, IIId or IIIa, IVb, and IVc. But it needs to be pointed out that one of the animals they studied, Doris, was the female participating in the present tests.

Table 6 presents the relative frequencies of each whistle

Table 2: Mean male response times (sec.)

Runs	Correct	Error	t Values of Difference	Total
II	2.71	2.72	.10	2.71
III	2.49	2.70	1.78	2.60
IV	2.62	3.57	2.79*	2.68
V	2.80	3.97	19.50*	2.82
VI	2.70	2.63	.38	2.69
VII	2.54	2.06	1.91	2.49
VIII, S ^D Exposed	3.03	3.27	.33	3.04
VIII, S ^D Masked	3.27	3.36	.67	3.32
IX	3.21	3.91	1.94	3.25
X	3.65	3.75	.14	3.67
XI	5.85	6.87	1.48	6.18
XII	6.32	6.87	1.30	6.57
XIII	4.28	4.38	.45	4.32
XIV	4.79	4.24	1.09	4.74
Total Runs	3.45	4.10	3.22*	3.60

* $p < .01$

Table 3: Contingency analysis of male's performance and female's whistle production.

Male's Performance:			
Female:	Correct	Error	Totals
Whistled	369	68	437
Did not whistle	83	54	137
Totals	452	122	574

Table 4: Contingency analysis of male's performance and female pulse train productions.

Male's Performance:			
Female:	Correct	Error	Totals
Pulsed	414	87	501
Did not pulse	38	35	73
Totals	452	122	574

Table 5: Contingency analysis of female's whistle and pulse train productions.

	Whistled	Did not whistle	Totals
Pulsed	425	76	501
Did not pulse	12	61	73
Totals	437	137	574

Table 6: Distributions of relative frequencies (%) of female and male whistles for each S^D condition and outcome of male's response.

Whistle Classes	Female Whistles					Male Whistles					Total Female and Male
	S ^D condition		Male's response		Total Female	S ^D condition		Male's response		Total Male	
	Flashing	Steady	Correct	Error		Flashing	Steady	Correct	Error		
Ia	15.6	12.5	12.4	21.1	14.2	25.2	19.8	19.6	32.6	22.5	17.5
Ib	5.2	8.3	3.6	18.0	6.6	4.9	7.7	2.8	18.5	6.3	6.5
Ic	7.2	5.2	4.4	13.5	6.3	5.8	3.9	3.7	8.7	4.8	5.7
Id	--	1.4	0.8	--	0.6	0.5	1.4	0.9	1.1	1.0	0.8
IIa	4.9	5.2	5.2	4.5	5.0	5.3	5.3	6.5	1.1	5.3	5.2
IIb	5.2	6.2	5.6	6.0	5.7	6.8	9.2	7.5	9.8	8.0	6.6
IIc	1.7	1.0	1.6	0.8	1.4	1.0	0.5	0.9	--	0.7	1.1
IId	2.3	2.1	2.8	--	2.2	--	--	--	--	--	1.3
IIIa	2.0	1.7	1.6	3.0	1.9	--	2.4	1.2	1.1	1.2	1.6
IIIb	2.3	1.4	1.6	3.0	1.9	1.5	1.0	0.6	3.3	1.2	1.6
IIIc	2.6	1.0	2.4	--	1.9	1.0	0.5	0.9	--	0.7	1.4
IIId	3.2	1.4	2.8	0.8	2.4	7.3	5.8	8.1	1.1	6.5	4.0
IVa	32.1	33.3	35.9	20.3	32.6	26.7	27.5	31.5	12.0	27.1	30.5
IVb	2.0	5.2	3.4	3.8	3.5	0.5	1.0	0.6	1.1	0.7	2.4
IVc	2.0	2.1	2.2	1.5	2.1	--	0.5	--	1.1	0.2	1.3
IVd	3.8	1.4	3.0	1.5	2.7	0.5	1.9	1.2	1.1	1.2	2.1
Va	3.8	7.3	6.4	1.5	5.4	4.4	4.8	5.3	2.2	4.6	5.1
Vb	0.3	0.7	0.4	0.8	0.5	1.0	2.4	1.9	1.1	1.7	1.0
Vc	2.6	1.4	2.6	--	2.1	6.3	1.9	4.4	3.3	4.1	2.9
VI	0.3	0.7	0.6	--	0.5	0.5	1.0	0.9	--	0.7	0.6
Misc.	0.9	0.3	0.8	--	0.6	1.0	1.4	1.2	1.1	1.2	0.9
Total Whistles	346	288	501	132	633	206	207	321	92	413	1046

Table 7: Classification of female's whistles
for male's correct and error responses
in each run

Frequencies of Whistles by Classes

Run	Male's Response	I				II				III				IV				V				VI		Misc.	Total Whistles
II	Correct Error					1				1 3 7				17 2 1 4 1								1			37 1
III	Correct Error					2				1				2 1 3 2				2 1							9 5
IV	Correct Error	1								1 3				4 6 5 1				2 5							27 1
V	Correct Error					1 1 3				1 1 5 2 1				23 2 1 1				3 1 2							47 1
VI	Correct Error	1				2 1				1 2 1 4 1				11 1 1											24 2
VII	Correct Error					1 4				2 2 1 2				16 1 4 1				3 2				2			38 3
VIII, S ^D Exposed	Correct Error					1 2 1 2								21 1 1 1				8 1 1					1		40 1
VIII, S ^D Masked	Correct Error	1 1				1				1				7 10 1 2				7 2 1							16 18
IX	Correct Error					1 1								31 1 1 1 2				1							37 2
X	Correct Error	1				5 1				1				21 1 2 1				3							33 3
XI	Correct Error	14 3 2 8 6 5				3 5 1 1 3				3 1				14 1 6 1				1					3		50 31
XII	Correct Error	15 7 9 1 12 14 11				7 7 3 4				1 1				3 1 2 1											52 47
XIII	Correct Error	10 2 4 7 3 2				1 4								1											22 12
XIV	Correct Error	22 4 6 3 1				13 3 2 2 1				1				10 1 1 1				3 1							69 5
TOTAL	Correct Error	62 18 22 4 28 24 18 0				26 28 8 14 6 8 1 0				8 8 12 14 4 4 0 1				180 17 11 15 26 5 2 2				32 2 13 3 2 1 0 0				3	4	0	501 132
Total Whistles		90 42 40 4				32 36 9 14				12 12 12 15				206 22 13 17				34 3 13				3	4		633

class produced by the animals for each S^D light condition and outcome of the male's response. After consolidating adjacent classes whose frequencies were prohibitively low, a χ^2 contingency test was performed on all whistles produced by the female in the two S^D light conditions. This yielded a χ^2 value of 13.37 which, for 12 degrees of freedom has a chance probability greater than .30, and thus provides no basis for considering the distribution of female whistles occurring in the two S^D conditions as different. The same test was applied to the whistles she produced during the S^D periods which the male responded correctly. This test resulted in a χ^2 value of 10.88 (10 degrees of freedom; $p > .30$), again indicating that the distribution of whistles was not reliably different for the two S^D light conditions, even when they should have been most distinct if they were influencing the male's paddle presses.

Though the female's whistles cannot be regarded as contingent on the S^D light condition, a statistically significant difference appeared between the distribution of her whistles when the male was correct and when he was in error ($\chi^2 = 69.84$, 8 degrees of freedom, $p < .001$). However, this difference is complicated by the even larger differences that appeared in the distribution of her whistles in connection with the changing experimental conditions. The distribution of her whistles for each outcome of the male's response is presented for each run in Table 7, which shows that when the acoustic barrier was completed in Runs XI through XIV there was a decisive change in the kinds of whistles she produced. The predominant

Table 8: Classification of male's whistles
for male's correct and error responses
in each run

Run	Male's Response	Frequencies of Whistles by Classes																				Total				
		I				II				III				IV				V					VI	Misc.	Whistles	
a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d							
II	Correct Error					1						1	1	7		11	2			1	2			2		28 1
III	Correct Error	2				1								1				1	2							8 5
IV	Correct Error			1		2						1	2			10			1	1	2			1		21 0
V	Correct Error					1	1						5			22 1			2	2	1			1		34 2
VI	Correct Error										1		4			12					1					17 1
VII	Correct Error												3			9 1			1	2		2	2			19 3
VIII, S ^D Exposed	Correct Error				1		2	3				1				11			2		3					23 1
VIII, S ^D Masked	Correct Error	2	1													5 6		2 1	1							11 13
IX	Correct Error					1							3			10 1			1							15 1
X	Correct Error					2				2						10 1			5			1	1			21 2
XI	Correct Error	9 8	1 6			4						3									1					14 20
XII	Correct Error	13 9	4 9	1 5		4 4	5												1							27 28
XIII	Correct Error	18 11	1 2	4 1		5																				28 14
XIV	Correct Error	19 1	2	6 1	2	14	2			2			1			1			2		4					55 1
Total	Correct Error	63 30	9 17	12 8	3 1	21 1	24 9	3 0	0 0	4 1	2 3	3 0	26 1	101 11	2 1	0 1	0 1	4 1	17 2	6 1	14 3	3 0		4 1		321 92
Total Whistles		93	26	20	4	22	33	3	0	5	5	3	27	112	3	1	5	19	7	17	3		5		413	

Table 9: Whistles emitted by female in response to male's whistles

Type and Number of Female Whistles in Response to Male's Whistles

Male Type	Whistles Number	None	I				II				III				IV				V				VI	Misc.
			a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d		
I	a	67	12	28	14	11		2																
	b	15			2	6	5	1	1															
	c	11	1	3	3	3			1															
	d	3	1				1								1									
II	a	12	4					4	2								1	1						
	b	28	6	1		1		13	7															
	c																							
	d																							
III	a	1																	1					
	b	1	1																					
	c	2	1												1									
	d	8	3										2	3										
IV	a	35	13					1	1	2	1	14		1				1	1					
	b	1											1											
	c	1											1											
	d	2	1												1									
V	a	9	6					1					1					1						
	b	4	1						1					1	1									
	c	3	1					1									1							
VI																								
Misc.	1							1																
Total Female Responses	204	51	34	23	20	1	19	14	1	2	1	2	3	21	2	1	4	3		1	1			

Table 10: Whistles emitted by male in response to female's whistles

Type and Number of Male Whistles in Response to Female's Whistles																									
Female Whistles			I				II				III				IV				V				VI		Misc.
Type	Number	None	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c				
I	a	87	23	48	6	6	1	1	2																
	b	33	8	13	11	1																			
	c	30	11	3	4	7		1	3										1						
	d	3	1					2																	
II	a	31	15	1			9	4	1		1														
	b	32	15	1	1		3	10	1					1											
	c	9	4											1		1			2	1					
	d	13	8					1						3		1									
III	a	12	9											3											
	b	12	10										1										1		
	c	10	3										1	5									1		
	d	13	1										8	2					2						
IV	a	194	97				4			4	1	9	61		1	1	4	2	7	1			2		
	b	23	8			1	2	1		1		1	6	2				1							
	c	14	6			1						1	3				1		2						
	d	15	10										1	1		1			1				1		
V	a	33	20				2			1							7	1	1	1					
	b	3	3																						
	c	12	6	1			1			1		1					1	1							
VI		3	2											1											
Misc.		3	3																						
Total Male Responses		585	263	67	22	15	2	18	27	3	5	1	2	22	88	3	1	4	14	5	15	3		5	

whistles shifted from classes III and IV to classes I and II, and it was the disproportionate increase in these whistles when the male was in error that was the chief source of the difference between her overall distributions of whistles for the male's correct and incorrect paddle responses.

The whistles produced by the male were also differently distributed when his paddle responses were correct and in error, but not for the two conditions of the S^D light. The χ^2 values for the two comparisons were 50.00 for the first; 6 degrees of freedom, $p < .001$, and 5.40 for the second; 9 degrees of freedom, $p > .80$. As with the female, this difference between the male's whistles when he was correct and incorrect was complicated by major changes in his whistles related to the changes in the experimental conditions. The distribution of his whistles for each run in terms of the outcomes of his responses is presented in Table 8. Along with the shift to predominantly class I and II whistles in Runs XI - XIV, he produced disproportionately more of these whistles when he was incorrect, and this was the main source of the difference between his whistles when he was correct and incorrect.

In spite of these parallels between the male and female whistles, they were reliably different overall ($\chi^2 = 38.50$; 9 degrees of freedom, $p < .001$). This overall difference was confined to their differences when the male's paddle response was correct, and this itself depended on her greater tendency to produce class IV whistles during Runs XI - XIV. Except for this, their whistles were remarkably

similar. This similarity is especially clear in examining the particular whistles they produced in response to each other, for usually the whistles of one would be answered by whistles from the other. The male responded in this manner to 55% of the female's whistles and she in turn responded to 74% of his, and such antiphonal exchanges comprising as many as 9 separate whistles were observed. All whistles emitted by the female in responses to the male are presented in Table 9, and those produced by the male in response to the female's whistles appear in Table 10. The analysis of these exchanges indicates that when the female whistled in response to the male whistles 48% of her productions were repetitions of the male's whistles, and that when the male whistled in response to the female 51% were repetitions of her whistles. These analyses demonstrate that not only were repetitions the most likely occurrences in these exchanges, but that when these rather close replications did not occur the next most frequent responses were from classes adjacent to the other animal's emissions. These findings can be taken as further implying similarity between adjacent whistle classes for the animals themselves, thus providing a measure of behavioral validity for the whistle classifications.

The conclusion that the animal's whistles did not participate in determining the male's paddle presses is further attested by comparisons of the whistles the animals produced during the 5 sec. Time In periods before the onset of the S^D light with those produced after its onset. These comparisons were made for the 116

Time In and 115 S^D periods of Runs VIII; S^D exposed, IX, and X, the results of which are presented in Table 11. Though this analysis is based on a sample of only a fifth of the Time In periods, it is apparent that the whistles produced by the animals during the Time In periods differ only slightly from those occurring in the S^D periods, primarily in the appearance of whistles of class II in the latter and the lowered frequency of whistles of any kind occurring in the former, in spite of their relatively longer durations. The whistles that did occur during these Time In periods appeared at approximately the same relative frequencies as their counterparts in the S^D periods over all runs. As there is no way in which the Time In whistles can have been contingent on the subsequent S^D light, the lack of any substantial differences between these whistles and those occurring after the onset of the S^D light provides additional evidence for concluding that the condition of the S^D light had little to do with the nature of the animals' whistle emissions.

However, as indicated above, there are several clear indications that the female's whistle productions were associated with the male's performance success. And even though there is no evidence that this association was based on differences in the types of whistles she emitted, there are, of course, many other ways in which her whistles could have been differentially related to the S^D conditions. Some of these possibilities were easily excluded. Examination of the occurrences of female whistles in S^D periods

following an error by the male or a change in the S^D condition did not reveal any systematic differences, nor were any differences found in the occurrence of multiple whistles by the female with respect to these conditions. However, when she was the first to whistle, which happened on 392 of the 574 recorded S^D periods (68%), there was a small but statistically reliable difference in the onsets of her whistles related to the condition of the S^D light. The means, standard deviations and number of these measurements are presented in Table 12. For the reasons discussed previously, the measurements were subject to underestimation by the human monitor's reaction time which, however, can be presumed to be fairly constant. The differences between the means of these measurements for the two S^D conditions when the male was correct was statistically significant ($t = 2.19$; 335 degrees of freedom, $p < .05$). None of the other pairwise comparisons of these means yielded statistically reliable differences.

The comparatively later average onsets of the female's whistles when the S^D light was flashing may have afforded a basis for the male's responses even though there was extensive overlap in the distribution of her whistle onsets under the two S^D conditions. This possibility was examined by partitioning the distribution of these measures for each run into earlier and later ranges in accordance with the number of S^D periods in each condition and then noting the male's response in the S^D period in which each whistle occurred. If the male had been keying his responses to the differences

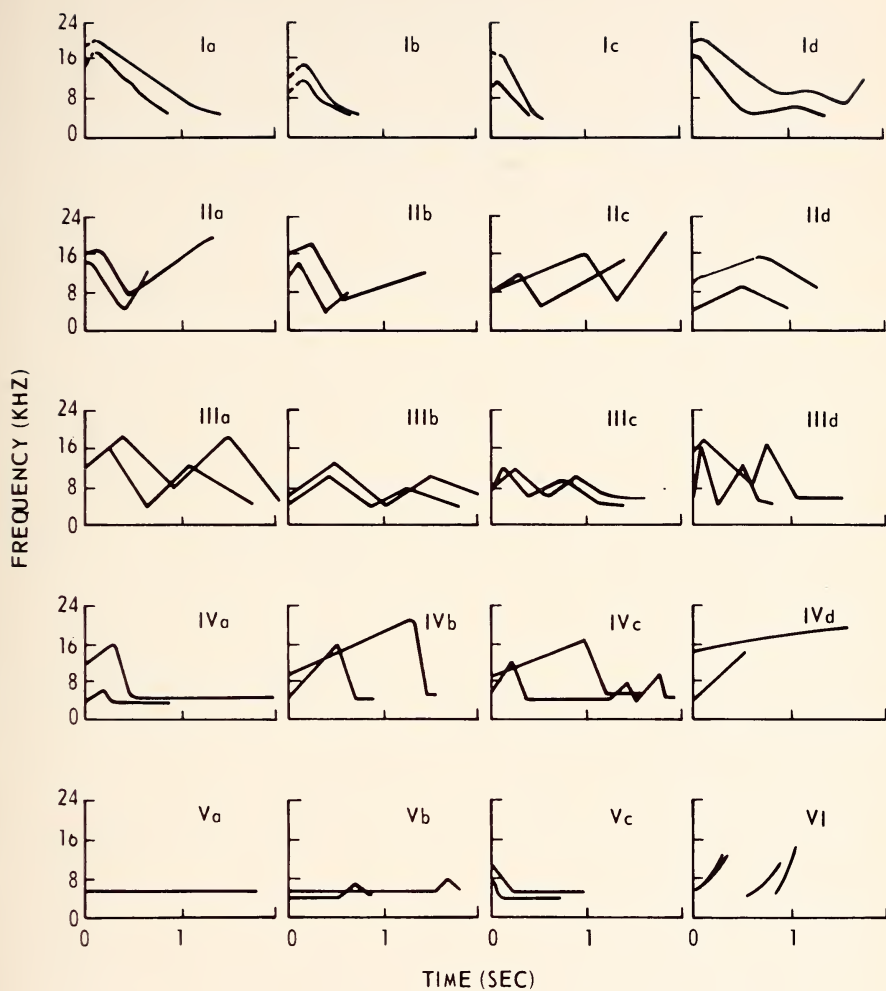


Figure 4: Extreme variants of each class of whistle contours.

in the onsets of the female's whistles then, as there were 206 S^D periods with the flashing S^D light, it would be expected that his predominant response to the 206 whistles with the latest onset times would be to press his left paddle. This tendency was observed, but only to a slight degree; he pressed the left paddle for 56% of these occasions. Conversely, he pressed his right paddle in 54% of the 186 S^D periods having the earliest whistle onsets.

The very weak contingency between the onset of the female's whistles and the male's responses would surely not provide a basis for the levels of performance success he actually achieved. But the overall timing of her whistles suggests that their contribution to the male's performance success was made by marking the onset of the S^D periods for him, and thereby serving to synchronize the actions of the two animals, some details of which are suggested below. This possibility is consistent with the strong likelihood that the differences in the average onsets of the female's whistles in the two S^D conditions arose from discrepancies in the control of the onsets of the S^D light in its two modes of operation. As indicated earlier, in the flashing mode the light was interrupted by periodically breaking its circuit, and so half of the applications of the control voltage (by which S^D period onset was recorded) to this circuit occurred during the "off" part of its cycle. This produced on the average a delay in the actual onset of the S^D light with respect to its recorded onset which did not occur in its steady mode of operation. If the difference in the timing of the female's

whistles were simply reflecting the actual differences in control of the different modes of operating the light, then the most remarkable aspect of these findings was not the difference in the female's whistle onsets but the extreme rapidity and precision of her reaction to the light, which unfortunately cannot be directly assessed because of the error introduced in establishing the onset of the S^D interval in the recordings on which these analyses were made. An almost comparable degree of temporal precision is also reflected in the timing of the male's whistles in the 256 S^D periods in which he responded to the initial whistles of the female just discussed. In the steady S^D light conditions the mean onset of his first whistles in response to hers was .64 sec. after hers, and in the flashing condition his whistle followed the beginning of hers by .80 sec. on the average.

Other features of the female's whistles that were examined, such as number of whistles per S^D period, changes in the whistles classes within trains of multiple whistles, proportion of S^D period in which whistling occurred, and the nature of her whistle response to the male's first whistle, did not reliably distinguish the two S^D light conditions. No evidence was found then of any relation between the female's whistles and the male's differential paddle pressing. The association of the female's whistles with the male's performance success therefore appears to be due to an indirect connection between the two, and the most plausible hypothesis for this was that the female's whistles, by being closely linked

Table 11: Comparison of whistles produced in Time In and S^D periods (runs VIII, S^D exp., IX; and X).

Whistle Classes	Whistles Produced by Female in:		Whistles Produced by Male in:	
	Time In Periods	S ^D Periods	Time In Periods	S ^D Periods
I a		1		
b				
c	1			
d				1
II a		1		
b		8		5
c		2		3
d	1	3		
III a	1	1		3
b			1	
c			1	1
d			1	4
IV a	12	78	6	32
b	3	2	3	
c		4		
d	1	2		
V a	4	11	7	8
b	2	1	1	
c		2		4
VI				1
Misc.	1	1		1
Total Whistles	26	117	20	63

with the onset of the S^D light, served to mark this critical event for the male.

Pulse Trains

Turning now to the female's emissions of pulse trains, it will be recalled that she emitted at least one in 501 (87%) of the 574 recorded S^D periods, and that on these occasions the male's performance was 83% successful. Furthermore, in the 73 S^D periods in which the female emitted no pulses, the male's performance fell to chance levels of success (52% correct), and 66 of those S^D periods occurred in Runs III, VIII; S^D Masked, and XIII where the female was either receiving no fish or no S^D light. In most of the S^D periods (81%) in which she did emit pulse trains, she produced only one. Multiple trains, ranging up to as many as 5 separate trains (counted as such when separated by more than .5 sec.) occurred most often during Runs XI and XII and were generally more likely in S^D periods in which the male's response was incorrect. In some degree the preponderance of multiple pulses in these conditions was no doubt associated with the longer durations of the S^D periods, due to the longer male response times (see Table 2). There were no reliable differences in the occurrence of multiple pulse trains for the two S^D light conditions, nor were there any significant differences related to S^D light mode in the durations of the intervals between offsets of the final pulse trains and the male's response. As indicated before, the male's response times cannot be considered different for the two S^D light

Table 12: Analysis of onset times of initial female whistles measured from S^D light onsets when female whistles before male, with respect to outcomes of male's response and S^D light conditions.

Male's Response:									
Correct			Error			Total			
S ^D Condition:	Mn.	S.D.	N	Mn.	S.D.	N	Mn.	S.D.	N
Flashing	.04	.63	180	.21	.96	26	.06	.66	206
Steady	— .10	.54	157	.05	.38	29	— .06	.52	186
Total	— .03	.59	337	.13	.72	55			

Table 13: Analysis of onset times of initial female pulse trains with respect to S^D light conditions and outcomes of male's response.

Male's Response:									
Correct			Error			Total			
S ^D Light:	Mn.	S.D.	N	Mn.	S.D.	N	Mn.	S.D.	N
Flashing	1.63	.96	204	1.67	1.19	39	1.64	1.00	243
Steady	1.20	.54	207	1.41	.74	51	1.24	.69	258
Total	1.17	1.13	411	1.52	.98	90			

Table 14: Analysis of onset times of initial female pulse trains measured from onsets of first female whistles, with respect to outcomes of male's response and S^D light conditions.

Male's Response:									
Correct			Error			Total			
S ^D Condition:	Mn.	S.D.	N	Mn.	S.D.	N	Mn.	S.D.	N
Flashing	1.74	.79	177	1.87	1.15	22	1.76	.81	199
Steady	1.34	.63	168	1.32	.62	33	1.34	.62	201
Total	1.55	.73	345	1.54	.85	55			

Table 15: Analysis of durations of initial female pulse trains with respect to S^D light conditions and outcomes of male's response.

Male's Response:

S ^D Condition:	Correct			Error			Total		
	Mn.	S.D.	N	Mn.	S.D.	N	Mn.	S.D.	N
Flashing	.90	.50	204	1.17	.64	39	.94	.58	243
Steady	1.60	.79	207	1.60	1.08	51	1.60	.86	258
Total	1.25	.78	411	1.41	.95	90			

Table 16: Analysis of pulse repetition rates (per second) of initial female pulse trains with respect to S^D light conditions and outcomes of male's response (Runs VII through XIV).

Male's Response:

S ^D Condition:	Correct			Error			Total		
	Mn.	S.D.	N	Mn.	S.D.	N	Mn.	S.D.	N
Flashing	21.2	11.34	131	26.0	17.54	35	22.2	13.06	166
Steady	25.1	10.95	133	32.1	10.11	41	26.7	19.20	174
Total	23.1	11.39	264	29.3	27.46	76			

Table 17: Analysis of elapsed time between onset of initial female pulse trains and male's response with respect to S^D light conditions and outcomes of male's response.

Male's Response:

S ^D Condition:	Correct			Error			Total		
	Mn.	S.D.	N	Mn.	S.D.	N	Mn.	S.D.	N
Flashing	1.74	.97	204	3.01	1.91	39	1.94	1.24	243
Steady	2.39	1.21	207	3.03	1.91	51	2.52	1.39	258
Total	2.07	1.14	411	3.02	1.91	90			

Table 18: Contingencies between simultaneous classification of durations and onset times of initial female pulse trains with respect to S^D light conditions and male's paddle response (excluding Runs VIII; S^D Masked, XI, and XII).

	Short pulse train		Long pulse train	
	duration		duration	
	Male's Paddle Response:			
	Left	Right	Left	Right
S ^D Light Condition:				
Flashing				
Late pulse train onset	102	3	21	0
Early pulse train onset	24	3	23	1
Steady				
Late pulse train onset	8	12	5	25
Early pulse train onset	3	21	10	113

conditions.

Though no differences could be found in the relation of the termination of the female's pulsing and the male's response that were connected with the experimental conditions, there were a number of other temporal features of her initial pulse train productions that were significantly different for the two S^D light conditions. Table 13 presents the average onset times of these initial pulse trains with respect to the onset of the S^D light in terms of the S^D mode and the male's responses. The differences between the overall onset times for the flashing and steady conditions were statistically distinct ($t = 5.39$, 499 degrees of freedom, $p > .01$). This level of distinctiveness also obtained for these differences when the male responded correctly ($t = 5.55$, 409 degrees of freedom; $p < .001$), but not when the male was in error ($t = 1.18$, 88 degrees of freedom; $p > .10$). The overall comparisons of these onset times for the different outcomes of the male's response also showed that her pulse trains began reliably later when the male went on to respond incorrectly ($t = 2.99$, 499 degrees of freedom; $p < .01$). This difference was most pronounced for the steady S^D conditions, though the correct vs. error differences in either S^D condition cannot be considered statistically significant by themselves.

It will be remembered that these measurements are subject to some error in the demarcation of the onsets of the S^D periods. However, in 400 of the 501 S^D periods in which the female emitted pulse

trains she also whistled, and these (first) whistles were found to be closely synchronized with the onset of the S^D light. Table 14 presents the average onset times of the female's initial pulse trains measured from the onset of her first whistles, separated as before according to the S^D condition and the male's response outcome. When her pulse train onsets are measured from her whistle onsets, the pulse trains the female emitted in the flashing S^D light condition are again found to begin significantly later than those in the steady S^D condition without regard to the male's response ($t = 6.00$, 398 degrees of freedom; $p < .001$). As before, when these differences are separated according to the outcomes of the male's response, only the differences occurring when the male responded correctly attained statistical significance ($t = 5.00$, 343 degrees of freedom; $p < .001$). When the male was in error, the differences yielded a t value of only .53. But in contrast to the first way of measuring her pulse train onsets, when these were reckoned in terms of onsets of her first whistles no difference appeared between pulse onsets in terms of the success of the male's response ($t = .08$).

The durations of the female's initial pulse trains were another feature which proved to be statistically different with respect to the S^D light conditions. These measurements are presented in Table 15 in terms of the outcomes of the male's responses. The durations of the pulse trains the female produced in the steady S^D condition were significantly longer than those occurring in flashing S^D periods,

Figures 5-18: Scatter plots of onset times vs. duration of female's

initial pulse trains for each run in terms of condition of S^D

light and outcomes of male's responses.

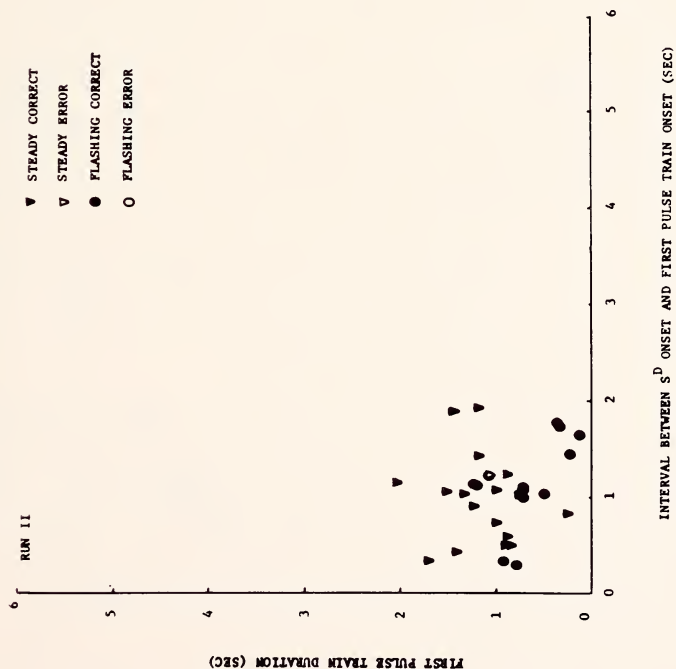


Figure 4

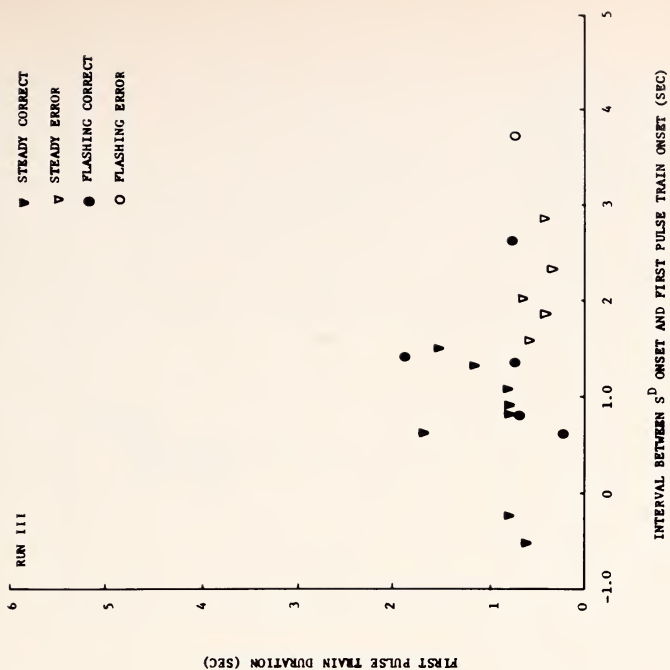


Figure 5

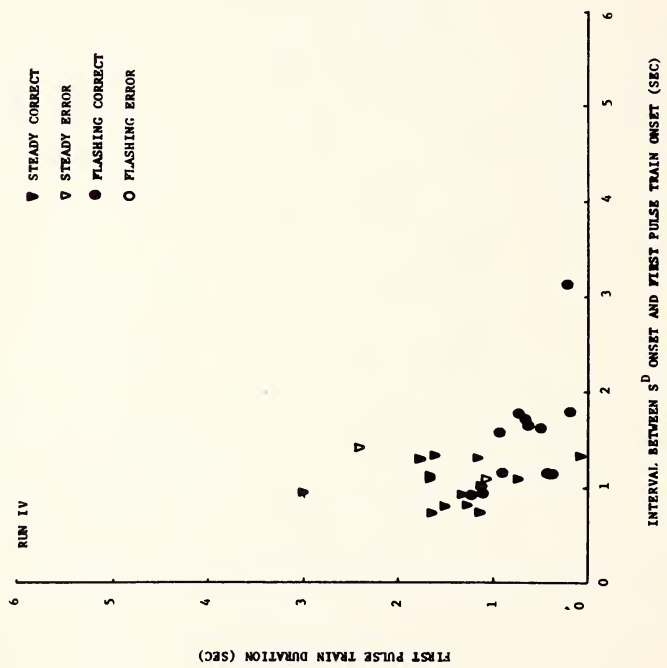


Figure 7

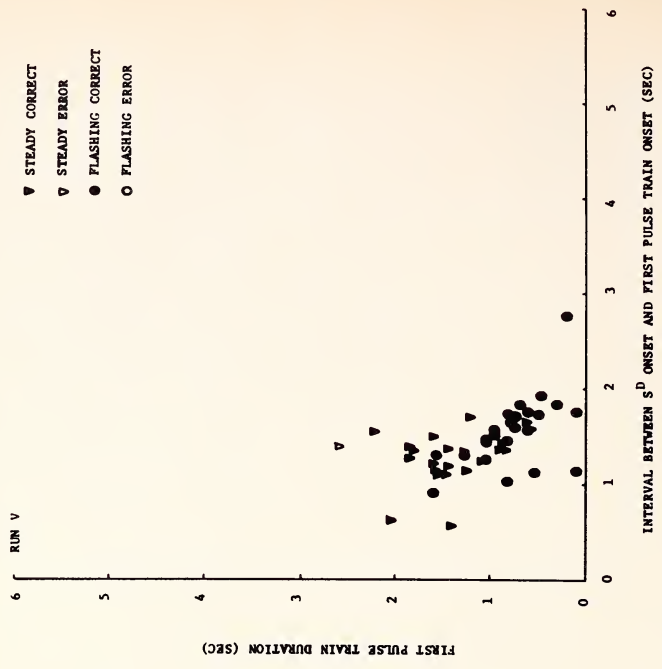


Figure 8

irrespective of the male's response ($t = 10.06$, 499 degrees of freedom; $p < .001$), and this difference was reliably maintained when both correct and incorrect responses of the male are considered separately (respectively: $t = 10.32$ and 2.33 , degrees of freedom = 409 and 88; $p < .001$ and $< .02$), but none of the other differences can be considered significant.

Figures 5 through 8 portray the distribution of these measurements for each run. For each of the initial pulse trains the female emitted in a given run, its onset time with respect to onset of the S^D light is plotted against its duration in terms of the mode of the S^D light and the outcome of the male paddle pressing response. Measured in this way, the onset times of pulse trains emitted under the two S^D conditions for those occasions when the male was correct were significantly different (at least at the .05 level of confidence) on 7 of the individual runs. When the pulse train onset times are referred to whistle onsets for those S^D periods in which the female both whistled and pulsed, these differences attained statistical significance in 8 of the individual runs. The comparable differences in pulse train duration were statistically reliable at the same level of confidence for all but one (Run III) of the individual runs.

Still another feature which distinguished these pulse trains under the two S^D conditions was the number of pulses per train. These were counted only in Runs VII through XIV, but within this sample there were on the average almost three times as many pulses

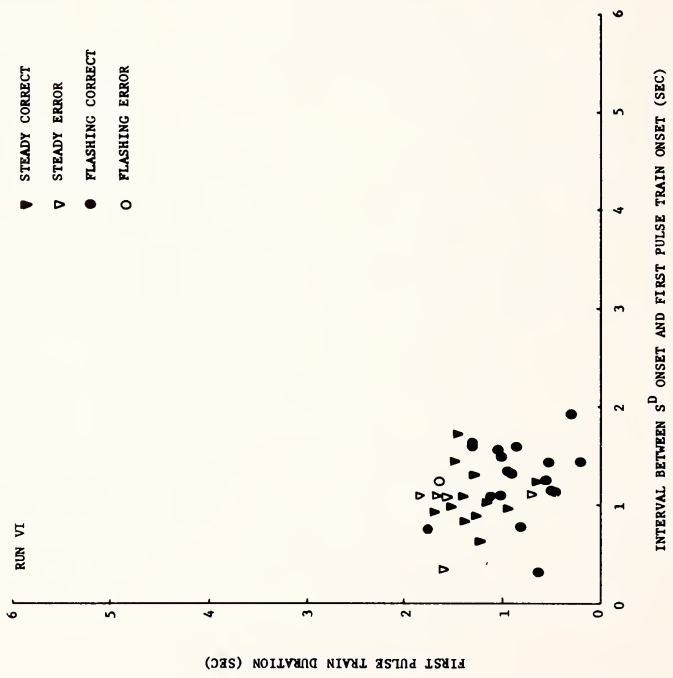


Figure 9

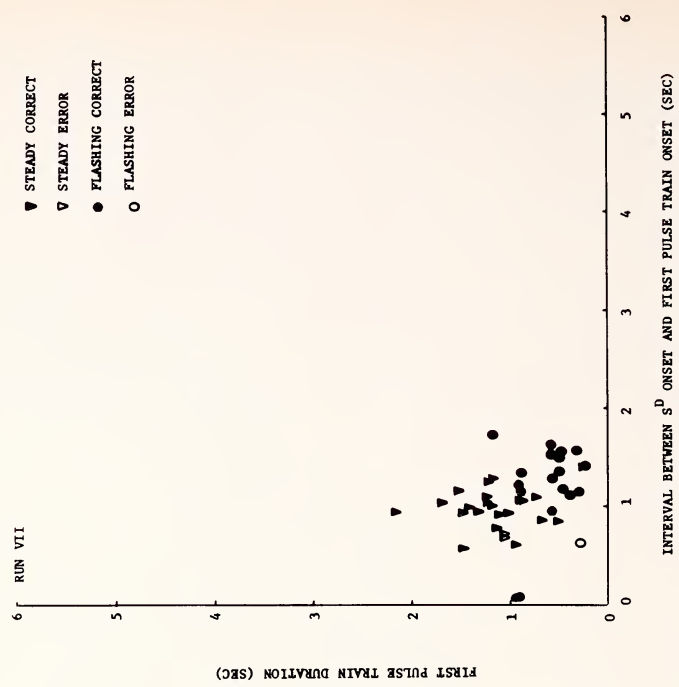


Figure 10

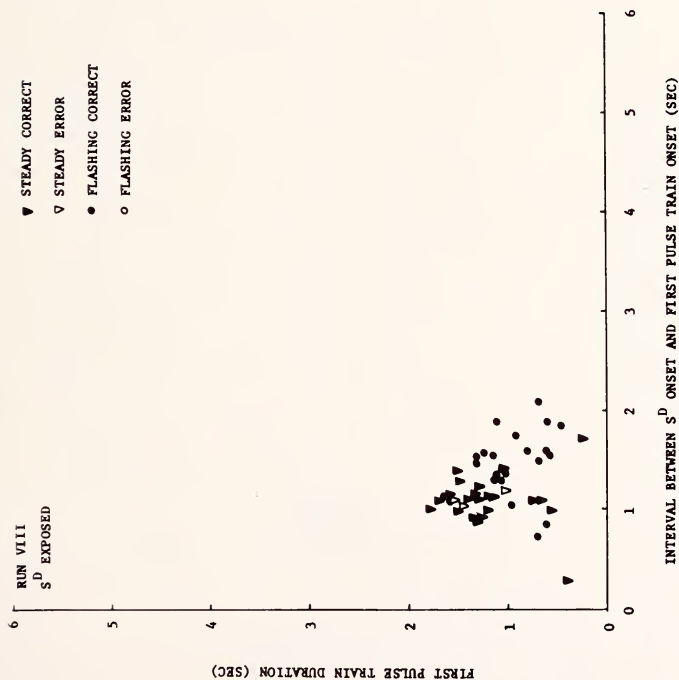


Figure 11

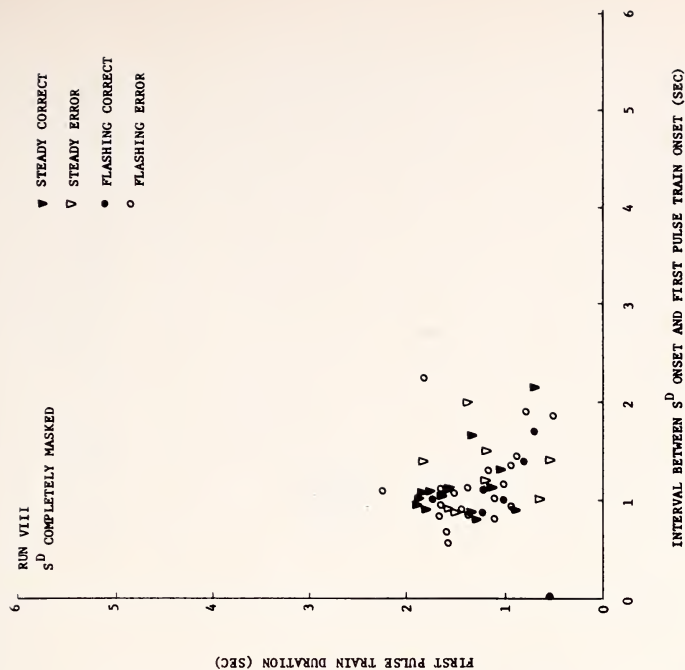


Figure 12

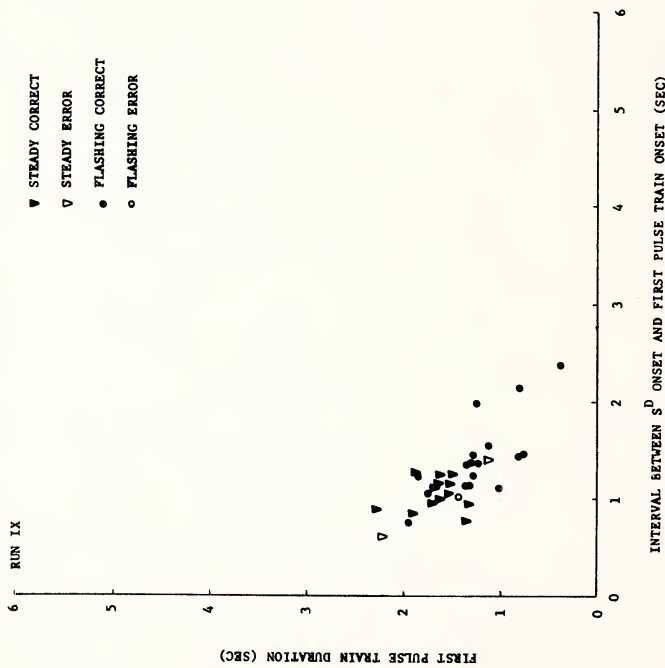


Figure 13

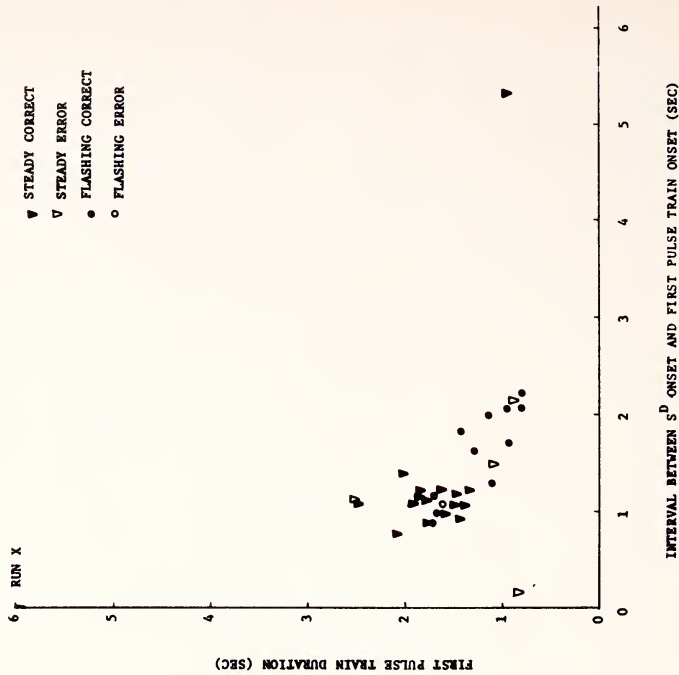


Figure 14

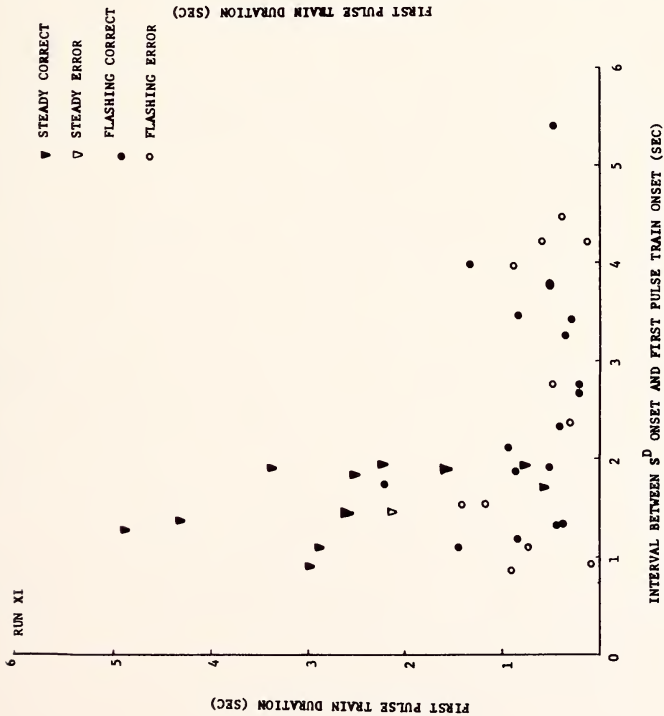


Figure 15

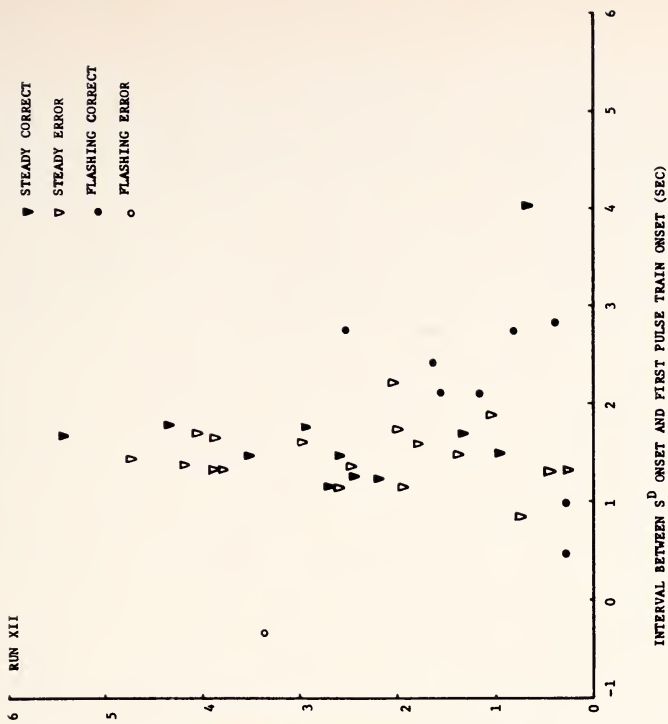


Figure 16

in the trains emitted in the steady condition of the S^D light as in the flashing condition. When the male was correct the average number of pulses in the steady and flashing conditions were, respectively, 46.6 and 18.1, and 47.7 and 21.7 when the male's response was incorrect. Both of these differences are reliable, as were the differences when the male was correct within each run considered separately, at least at the .02 confidence level, except for Run VIII when the S^D light was completely masked. As the magnitude of these differences in number of pulses per train is not proportional to those obtaining for their durations, it follows that the average pulse repetition rate would be higher for those pulse trains emitted in the steady S^D light condition. This was indeed found to be so, though within each train the repetition rate was in fact not constant. Usually the rate of pulsing was higher at the beginning of the trains, most often falling thereafter to a fairly uniform rate for the remainder of the train.

Table 16 presents the average pulse repetition rates for these pulse trains over their entire durations. All comparisons are statistically reliable at the .05 level of confidence or beyond except for the difference in the flashing condition between those emitted when the male was correct and in error. As these animals often emit pulse trains at rates of several hundred pulses per second, the repetition rates of the emissions under consideration are all uniformly low, and not at all typical of their "creaking door" pulse productions. Lilly and Miller (8) have suggested that the

pulse emissions of these animals having the low repetition rates found in the present analysis may be social rather than echo ranging actions.

Discussion: Determinants of Male's Responses
and Further Research Requirements

An overall characterization of the pattern of these differences would be to say that the pulse trains emitted by the female in the flashing condition of the S^D light were more "tentative" or more "hesitant." They began later, they were briefer, and they consisted of fewer pulses emitted at lower rates than the pulse trains emitted in the steady S^D light conditions. But though these differences were more pronounced for those S^D periods in which the male's responses were correct, it does not necessarily follow that the differences in the male's responses were determined by these differences in the female's pulse trains, nor that if the male had been keying his responses to her emissions that it was these features of her productions which were critical for him.

However, the results of the present study do contain evidence of some connection between the nature of the female's pulse emissions and the male's behavior that is at least consistent with the possibility that his responses were in some degree governed by her pulse train productions. Table 17 presents the average duration of the interval between the inception of the female's initial pulse train and the male's response. In spite of the previously mentioned lack of reliable differences in the timing of the male's responses

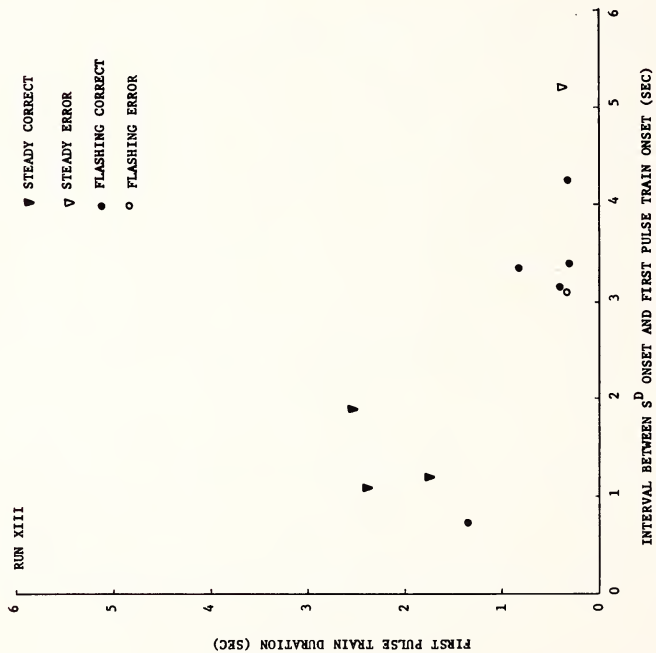


Figure 17

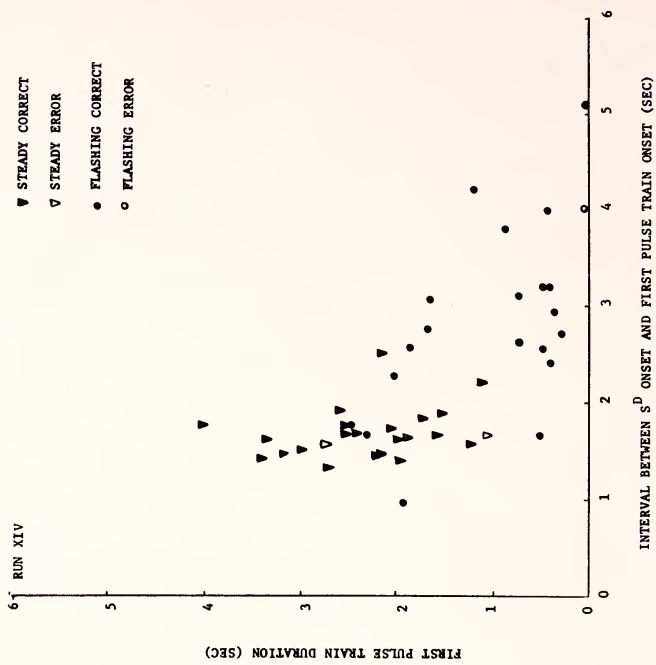


Figure 18

with respect to the conditions of the S^D light, the overall elapsed time between onset of the female's pulsing and his response was significantly longer when the S^D light was in the steady mode ($t = 4.9$, 409 degrees of freedom; $p < .01$). This was also the case when the male was correct ($t = 6.01$, 409 degrees of freedom; $p < .01$) but not when he responded incorrectly ($t = .05$, 88 degrees of freedom; $p > .50$). All differences between these intervals with respect to the outcomes of the male's responses were reliable at the .05 level of confidence at least. Considering each run separately, the differences in the average duration of the female's initial pulse train, when the male was correct, reached at least the .05 confidence level on all except Runs III and VIII; S^D Masked.

These differences in the timing of the male's responses with respect to the female's pulse train onsets for the two S^D conditions are directly linked to the comparable differences in the onsets of her pulsing. However, the leading problem in the question of the contingencies between the male's response and the female's pulse emissions is whether the demonstrated statistical differences in her pulse trains were in fact sufficiently distinct to sustain the high level of performance success the male actually achieved. Leaving aside the closely related problem of the male's ability to discriminate these different properties of the female's pulse trains, some evidence of the contingency between the female's pulse emissions and the male's responses can be gleaned from dichotomizing the distributions of the measurements of these properties according to the nature of the observed differences, and then noting what response

of the male was actually associated with each pulse train. That is, if in a given run the male had been responding to differences in the durations of the female's pulse trains, then his predominant response to the longest durations should be to press his right paddle. And if the pulse train were dependent on the condition of the S^D light, then the distribution of the duration measurements could be partitioned into "long" and "short" in accordance with the number of occurrences of each S^D condition, so that the number of "long" durations would be equal to the number of steady S^D conditions for that run.

Though the basis for partitioning the distributions imposes a great strain on this line of reasoning, it was applied to the onset and duration measurements in the recorded data, except for Runs VIII; S^D Masked, XI, and XII where the presumed chain connecting the condition of the S^D light to the male's response was broken for one or another reason. These dichotomies were established for each run separately, as Figures 5 through 19 demonstrate that the ranges of these measurements changed markedly, especially during the later runs. The tallies, over all runs, are presented in Table 18.

In the main, it is clear that the categories of onsets and durations of the female's pulse trains do tend to be associated with one another, and with the condition of the S^D light in about equal degree. However, the point of most interest is the contingencies between these features of the female's pulse trains and

the male's paddle pressing responses. Table 18 indicates that in the 125 S^D periods in which the female pulse trains were classified as having both "late" onsets and "short" durations the male pressed the left paddle 110 times (88%), and that in the 147 periods in which her pulse trains were both "early" and "long" he pressed the right paddle 114 times (78%). When the classifications of these properties of the female's pulse trains were not concordant (102 S^D periods) the male's paddle presses showed no systematic tendencies; 49 right and 53 left paddle presses. If these findings are taken as measuring the degree of the relation between the male's paddle responses and these features of the female's pulse trains, and if it is assumed that nothing else influenced his responses, then his performance success would have been determined by the degree to which the female's productions were contingent upon the conditions of the S^D light. On these assumptions, 246 of the 374 responses made by the male (66%) would be expected to be correct. However, he actually achieved a 91% level of success (341 correct responses). The largest part of this discrepancy is due to the high level of success (89% correct) the male attained in the 102 S^D periods in which the onset and duration classifications of the female's pulse trains were not in accord. Had his responses been completely determined by these classifications of the female's productions he would have had only a chance (50%) level of success. For the 272 S^D periods in which these classifications were concordant, his expected level of performance would have been 72% correct, whereas

he actually obtained 92% level of successful performance.

However, fragile the logic of this analysis may be, it does at least indicate that a large part of the male's performance was consistent with these excessively simple assumptions, though it is clear that other factors and less simplistic reasoning must be sought in order to account for his performance, particularly when the durational and onset features of the female's pulse trains are apparently inconsistent. Aside from this particular analysis, the overall results of this investigation quite firmly indicate that the male was discriminating something in the pulse train signals generated by the female, and that the differences observed in the onsets, durations, and repetition rates of these pulse trains were in some degree available for his discrimination. The question of whether it was these features that were governing the male's responses is moot on the present evidence. Other possible sources of differences in her pulse trains which might have contributed to the determination of his behavior could not be examined in the present investigation. For instance, there might have been spectral differences in the individual pulses that were associated with the conditions of the S^D light, but as the recordings of her emissions were obtained from a fixed hydrophone location in the experimental chamber, the recorded frequency characteristics of her productions were contaminated by her changing position. This consideration is also involved in assessing another, very plausible, source of differences in the female's productions. Earlier reference has been

made to the quite different patterns in the female's approaches to her two paddles. As her initial pulse trains were characteristically emitted during these approaches, it is clearly possible that the consequent acoustical differences in the signals reaching the male provided the basis for his discrimination and that the differences that have been established were either redundant or irrelevant. Differences arising from the contrasting female's positions were clearly evident in the recordings obtained from the hydrophone in her side of the tank (see Fig. 1), but the amplitude levels of her signals reaching the hydrophone on the male's side were not sufficient to permit reliable analysis.

Further "playback" experiments involving the systematic manipulation of these features are in preparation which can be expected to eliminate some of these possibilities, and to provide in the process a specification of the acoustical properties of the female's emission critical for the male's discrimination. With this in hand it will then be possible to pose appropriately the question of the basis of the female's signalling actions, i.e., why did she emit these signals? There are three possible types of answers to this question that may be entertained. One answer, by far the most interesting, is "simply" that the nature of these animal's signalling system is such that their referential scope subsumes the arbitrary environmental events of this investigation, so that when the need arose for communicating this information effective means for its transmission were already available. If that were so then it could

be expected that this signalling system would also permit the transmission of other information of at least comparable complexity. This possibility can be fairly directly assessed by systematic changes in the test situation which involve different kinds of arbitrary environmental events.

Another possibility, which is also very interesting but in a widely different sense than that just discussed, is that the female became conditioned to produce differential phonatory actions in the course of the necessarily complex preliminary training leading up to the actual tests, and the male concurrently learned to exploit these differences in keying his actions to them. The nature of the preliminary training was such as to easily provide the opportunity for this possible learning, especially in regard to the male. However, it can be quite directly tested by requiring the animals to reverse their established roles, or by replacing each of them with an inexperienced animal.

These procedures would also provide information relevant to the remaining possibility that either one or both of the animal's conduct derived from genetically fixed patterns of behavior or was based on their experience prior to this experiment. It is quite possible that the female's pulse trains were orientation responses to the S^D light and that the inherent differences in the S^D light conditions were reflected in her orientation to them. It is also possible that in these animals' free ranging lives they become capable of exploiting the echo ranging actions of others for gaining

information about their environments, and that this capacity was the basis of the male's performance. However plausible, a key difficulty with the notion that the female's productions were essentially orientation responses was the finding that they were much more susceptible to the extinction effects of Runs III and XIII than her actual paddle presses and that neither animal showed any indication of producing these responses to their Time In lights. Whatever the outcome of these future investigations, the present evidence showed these animals capable of quite readily shifting to acoustical control of a rather complex behavioral task originally performed to visual cues. This capacity for cross modal transfer of training is in itself worthy of further investigations, for it has been argued that it does not tend to occur in non-humans and that it is fundamental to the nominative function of man's languages (4).

ABSTRACT

This is a report of an investigation of the capacity of a pair of bottlenose dolphins to perform a cooperative task which required the acoustical transmission of information about an arbitrary visual event in the environment of one of the animals. Each animal was first trained to press one of two paddles, depending on the state of a light signal. Next, while housed in adjacent enclosures they were required to coordinate their actions in a fixed sequence and within fixed time limits. Then the light signal to the animal required to respond first was removed and visual contact with the other animal and its light eliminated.

The pair continued to perform successfully as long as they were in acoustical contact and the light signal to the one animal was provided. Their performance success was found to depend directly upon the emission of pulse trains by the animal receiving the light signal, although it was also found to be indirectly connected with its emission of whistle signals. The specific nature of this dependency could not be determined.

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DISCUSSION

par

J. C. LEVY

Je n'ai, au sujet du dispositif expérimental, aucune observation particulière à formuler.

Je remarque seulement le soin avec lequel l'auteur a établi une méthode d'entraînement de façon à faire comprendre aux animaux les tâches de plus en plus compliquées que l'on attend d'eux.

D'autre part le dépouillement des tableaux résultats aurait demandé des moyens matériels dont je ne dispose malheureusement pas.

Je me bornerai donc à évaluer d'une façon quelque peu philosophique la valeur des informations transmises d'un animal à l'autre.

Si j'ai bien compris, les informations transmises au mâle par la femelle portent sur les deux points suivants :

Un top de départ.

Une indication binaire qu'il n'est pas possible pour le moment d'explicitier d'avantage : la femelle dit elle au mâle : "feu clignotant" ou : "feu continu" ou bien encore : "Droite" ou "Gauche", non seulement il est impossible de le savoir, mais encore il est très vraisemblable que cette question n'a pas de sens.

Les autres indications, celles qui ne varient pas d'une épreuve à l'autre, telles que les indications de délai d'exécution du travail, sont acquises par l'entraînement et non forcément transmises d'un animal à l'autre.

La première des suppositions faites par l'auteur relativement à la nature des signaux me semble la plus vraisemblable : il s'agit d'utilisation aux fins de transmission d'un animal à l'autre des signaux d'orientation, ce que l'on ne sait pas, c'est si ces signaux sont intentionnellement émis : pour le mâle, ou s'ils sont simplement observés par ce dernier : il y a toutefois un dialogue, si l'on admet que la femelle émet des sons différents suivant que le mâle se trompe ou non. Cela prouverait une chose : la femelle guide volontairement le mâle, et ce dernier ne se contente pas simplement de l'observer.

Nous pouvons donc introduire une autre information binaire :
"Tu ne te trompes pas" ou : "Tu te trompes".

Cela me rappelle le jeu bien connu de "cache tampon" dans lequel les indications : "bon" ou "mauvais" se traduisent par "chaud" ou "froid".

A ce moment je me pose une question : dans quelle mesure un animal peut-il transmettre à un autre des données relativement plus complexes qu'une simple indication binaire ?

Pour tenter de répondre à cette question, j'aimerais suggérer un autre procédé expérimental :

Un seul animal serait préalablement entraîné à effectuer un travail d'une difficulté modérée, ensuite on essaye de lui faire enseigner cet exercice à un autre animal, ce dernier ne sera peut-être pas tout à fait novice, mais il sera beaucoup moins entraîné.

Pour bien faire comprendre ce que pourrait être la méthode expérimentale, je vais encore parler du jeu de "cache tampon" et distinguer trois cas.

- 1°) L'élève sait simplement qu'il y a un objet quelque part, caché, il ne reçoit aucune indication, il cherche et tâtonne jusqu'à ce qu'il trouve.
- 2°) L'élève ne reçoit que des indications binaires (c'est le cas du jeu) le maître lui dit : "Froid" ou "chaud" ce qui veut dire "Mauvais" ou "Bon" où correspond chez l'animal à des sons différents.
L'élève cherche encore et tâtonne toujours, mais moins longtemps que dans le premier cas, cette différence devrait être évaluée.
- 3°) Le maître explique exactement à l'élève où se trouve l'objet, et celui-ci le trouve sans aucun tâtonnement.

Dans le cas deux, le maître doit savoir où se trouve l'objet, et pour guider son élève, ne fût-ce que par des signaux binaires, il doit avoir présent à l'esprit le trajet à suivre pour atteindre l'objectif.

Cela exige de lui une très grande aptitude à la synthèse, mais il est certain que les animaux supérieurs, capables d'élaborer des programmes d'action complexes sont capables d'abstraction et de généralisation ; la question qui se pose alors est la suivante : dans quelle mesure ces animaux peuvent-ils se communiquer des données de nature plus générales que de simples ordres d'exécution ?

La différence entre les cas deux et trois permettrait de trancher la question.

Si l'animal est incapable de comprendre qu'il lui faut aider un congénère, s'il est incapable de concevoir dans son ensemble un plan d'action la deuxième opération n'est pas possible.

Pour que la troisième opération soit possible, il faudrait (nous ne pouvons ici ne parler qu'au conditionnel) que le langage de l'animal soit assez évolué pour lui permettre d'exprimer sa pensée, c'est-à-dire quelque chose de plus général que de simples ordres d'exécution de mouvements élémentaires.

Le diagramme (fig. 1) permet de mieux comprendre ce principe.

L'on distingue en S les centres sensitifs et en M les centres moteurs. Les perceptions sensitives provenant de l'environnement, parviennent en s les ordres moteurs partent de m pour atteindre l'environnement.

De S à M les signaux peuvent emprunter différents trajets correspondant à des niveaux d'intégration de plus en plus élevés, partant des réflexes élémentaires pour aboutir à des opérations de synthèse et des programmes d'action de plus en plus évolués.

Les centres sensitifs effectuent, à partir des perceptions élémentaires des opérations de synthèse permettant à aboutir à des "concepts" de plus en plus généraux, en passant par le plus courant de tous : l'identification d'un objet à partir de ses multiples aspects.

Les centres moteurs effectuent un travail d'analyse en élaborant des programmes et sous programmes de plus en plus détaillés pour aboutir à des ordres élémentaires donnés aux muscles.

A tous les étages il y a contrôle des centres moteurs par les centres sensitifs.

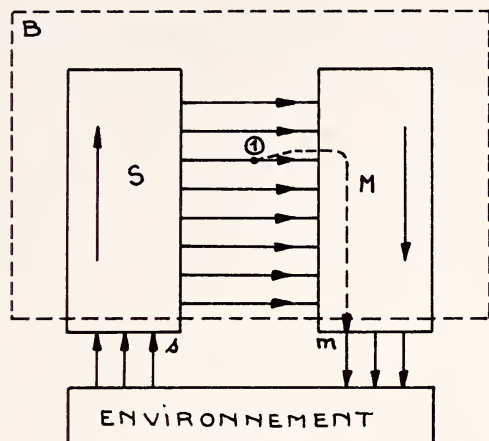
Supposons par exemple que nous apercevions un objet comestible :

- Programme d'action : "le manger",
- Programme de détail : approcher notre main pour le prendre,
- Contrôle par les centres sensitifs à un niveau inférieur : ne refermer notre main que quand elle aura atteint l'objet.

De l'animal nous ne connaissons que ce qui entre en s et sort en m, autrement dit, nous ne connaissons de lui que son comportement, le reste, représenté dans le carré B constitue une boîte noire.

L'homme, au contraire doué du langage peut par exemple, nous expliquer ce qui se passe en (1) et l'extérioriser directement par des réactions accessibles en m.

Fig. 1



Par exemple, supposons qu'un animal désire atteindre de la nourriture hors de sa portée.

S'il effectue des tentatives infructueuses nous comprendrons par son comportement quelle est son intention, même s'il ne peut pas la satisfaire.

Mais s'il juge par avance tout effort inutile, il ne lui sera pas possible de dire, comme nous saurions le faire, j'aimerais l'attraper, mais je ne le peux pas.

Il faut toutefois faire une exception pour les animaux domestiques comme les chiens et les chats qui savent se faire comprendre par des jeux de physionomie compréhensibles par l'homme, ceci dans le but de se faire aider par ce dernier.

Mais les dauphins, à ma connaissance, ne sont capables d'aucune mimique.

Quand un homme connaît bien un animal, il peut expliquer les raisons de son comportement ; l'homme substitue alors son intelligence à celle de l'animal et peut exprimer, ce que ce dernier est incapable de faire, les mobiles de tel ou tel comportement.

Cela n'est pas du langage : c'est de la sympathie, prise au sens étymologique du mot. Cette sympathie peut exister entre être humains, entre l'homme et l'animal et même entre l'homme et la machine.

Si je rencontre un homme tel qu'il n'y ait entre lui et moi aucune "sympathie", son comportement qui m'est seul accessible me surprendra, mais si nous possédons un langage commun, le sujet sera en mesure de m'expliquer les mobiles de ce comportement, l'animal ne le peut pas. La machine le peut quelquefois quand elle a été prévue pour cela.

Mais inversement, je ne peux pas expliquer à un animal les raisons de mon comportement, et si ce dernier en est surpris, il adoptera à mon égard une attitude craintive ou agressive. Tous les dresseurs ou dompteurs savent cela, leur art consiste à sympathiser suffisamment bien avec la bête pour ne pas la surprendre par un comportement inhabituel pour elle.

Les rapports entre explorateurs et peuplades sauvages posent le même problème, il en est de même entre gens civilisés parlant la même langue, mais trop différents l'un de l'autre pour avoir le loisir de s'expliquer suffisamment clairement. Mais toutes les fois qu'une telle explication est possible l'homme est pour l'homme plus qu'un être accessible seulement de l'extérieur et dont le comportement est plus ou moins bien prévisible. En est-il de même des animaux supérieurs appartenant à une même espèce ? S'ils vivent en bonne entente, c'est qu'ils sympathisent, c'est-à-dire que leurs comportements sont semblables et compréhensibles l'un pour l'autre. Mais si l'on arrive à leur créer des situations imprévisibles, telles que la dissimulation d'un objet en un endroit qu'ils ignorent, dans quelle mesure leur langage peut-il suppléer à ce défaut de prévisibilité ?

Bien entendu, la recherche d'un objet dissimulé inspiré d'un jeu de société pour humains n'est citée ici que comme exemple, il n'est pas question d'en faire un programme d'expérience.

Si une expérience précise est faite dans ce sens elle devra être prévue par des spécialistes et menée d'une façon progressive en dosant les difficultés de façon à ne pas risquer de demander à un animal plus que ce que l'on pourrait à priori espérer de lui.

L'expérimentation parfaitement bien conduite de Monsieur J. BASTIAN constitue un premier pas qui nous ouvre dans un domaine nouveau et encore inconnu, des perspectives considérables.

INTRASPECIFIC TRANSFER OF INFORMATION
VIA THE PULSED SOUND
IN CAPTIVE ODONTOCETE CETACEANS

by
M. C. CALDWELL and D. K. CALDWELL

The two species of captive odontocete cetaceans with which we have worked principally are the apparently more primitive Amazon freshwater dolphin, Inia geoffrensis (Blainville), and the apparently more recently-evolved marine Atlantic bottlenosed dolphin, Tursiops truncatus (Montagu). The bulk of this discussion will be centered on these two species. Brief mention will be made also of the pulsed sound emissions of the Pacific striped dolphin, Lagenorhynchus obliquidens Gill.

By the use of the terms "social signal" or "communication", no intent is implied for the animal using the signal. Unless positive evidence is presented to the contrary, we must regard all sub-human signals as non-purposeful on the part of the animal giving the signal. Social signals are actions elicited by an emotional state and are meaningful only in that another animal is able to receive them. The reception may be through either a genetically predetermined neural substrate or the ability to become conditioned to specific physical characteristics of the signal.

In our work up to this point, we have begun with two basic assumptions, neither of which has been experimentally proven but which are based on behavioral correlations.

The first of these assumptions is that the pulsed sounds emitted by cetaceans are of two categories: (1) a click train of pulses emitted in obtaining environmental information, usually referred to as echolocation, and (2) rapid bursts of pulses emitted in an emotional context. After working with captive odontocete cetaceans for some time, many, but not all, workers fall into this line of thought and the distinction is either implied or stated (see, for example, 4, 15, and 25). The physical characteristics that divide the two categories of pulsed sound are in need of more analysis as it would seem that there are differences in the two classes of sounds other than repetition rate.

Although we are intensely interested in knowing whether a sound is used in echolocation or an emotional context, for practical purposes of this discussion on the transfer of information via the pulsed sounds, an echolocation train carries just as much information content as a sex yelp. It is just different information.

Consequently, a specific type of pulsed sound given in the proper context may come to mean "food" (approach) or "danger" (flee). A porpoise need not concern itself with the "why" or "how" of the sound, only the "what," "when" and "where."

The second assumption is that any sound discrimination that we can make, an experienced dolphin or porpoise can make as well or better. This assumption has the advantage of placing us in the group with the majority of our colleagues, most of whom also tacitly assume that this is so.

In actuality, all of the research on sound discrimination in dolphins and porpoises has resolved around the ability of these cetaceans to emit, receive and discriminate echoes of the click-train type (see, for example, 14 and 19, for reviews). There are no published reports of experimental research that has been directed, for instance, toward the ability of cetaceans to discriminate differences between two frequencies, temporal pattern, intensity, or duration of sounds. However, the fact that Cetacea are frequently trained on the basis of different sound cues would indicate that their auditory discrimination faculties are excellent.

In the higher orders of mammals, particularly, it is very evident that most stimuli are perceived and reacted to with regard for the total stimulus situation. A "squawk" emitted in one context may possibly be perceived as a mild protest, in another as a threat, or again as an invitation to play. Marler (18) has strongly emphasized this point in primate behavior studies by noting that the most striking generalization that could be advanced from his survey of communication in monkeys and apes is the overwhelming importance of composite signals.

It would be misleading to restrict our observations on the transfer of information in cetaceans via the pulsed sounds to the sound alone, and to present the sound as a discrete and self-contained unit. It would be particularly misleading not to emphasize that in Tursiops truncatus the pure-tone whistle component is contributing heavily to the ongoing transfer of information in conjunction with the pulsed sound.

One of the major bits of information carried by the whistle is the identity of the animal doing the whistling (7). Responses of other animals in the group may be determined solely on the basis of this identification. Heightened emotional states are indicated by increases in the number of "signature" whistles in a given time period, and their intensity. Also, although the general contour remains almost identical, the whistle is emitted more rapidly. Some animals tend to vary their basic whistle contour more than others, but the variation is usually infrequent and the observer has no trouble in identifying the signature whistle peculiar to any particular animal. Many animals with which we have worked have never varied the basic contour regardless of the extreme conditions to which we have subjected them.

Visual, tactile and probably gustatory signals are being fed to the recipient in conjunction with the sound signals. The tactile senses in Tursiops truncatus play a particularly heavy part in the communication of information, ranging in precopulatory behavior from a gentle mouthing or rubbing to the violent head crashing that frequently precedes copulation (Fig. 1). This violent head bumping has also been reported in the precopulatory behavior of the Pacific pilot whale (2).

The physical environment is also providing a steady input of changing information. The time of arrival of each of these signals in relationship to the others is a factor that must be evaluated somewhere in the nervous system. The entire subject of animal communication is in fact so highly

complex that we can only hope to chip away at the edges of the problem.

Behavior studies are difficult to keep from being partly subjective and this one is probably no exception. This type of study is particularly so as sounds that seem meaningful or obvious to the investigator are the ones selected for study. Therefore, each sound that we will be discussing is probably an extreme, either in the sense that it is definitive enough for us to have detected, or it was emitted in a situation which commanded our special attention. There are probably intergrades of all the pulsed sounds as shown for the rhesus monkey (22). Because these intergrades are meaningless to us at this point, our minds tend to pass over them. The only solution to this defect is a continuing exposure to the animals in their environment. Animals are exposed to their environment 24 hours a day, 365 days of the year, and have many more "trials" at learning the meaning of signals than do their human observers. Also, the rewards for correct responses and punishments for incorrect responses are immediate (Fig. 2). Learning takes place quickly under these conditions.

In the following discussion we will be leaning heavily on the use of sound spectrograms. Although the Kay sonagraph machine makes graphs which show us many of the physical characteristics of sound that we cannot determine by ear or adequately describe, the human ear clearly detects nuances of sound that are not demonstrable on a sonagram (3, 21). There are also sounds emitted in a medley of other sounds that the ear is able to follow selectively (the "cocktail hour" effect) which do not lend

themselves to suitable sonographic reproduction.

RECORDING AND ANALYZING EQUIPMENT

The underwater sounds reported upon herein were recorded with an Atlantic Research Corporation model LC-57 hydrophone having a flat frequency response (± 2 db) to 20,000 cycles per second. The signal from this hydrophone was fed through a special preamplifier built for the system by William W. Sutherland of the Lockheed-California Company, Burbank, to a Uher model 4000 Report-S tape recorder operating at a tape speed of 19 cm (7.5 inches) per second. At that tape speed the recorder had a flat response of 40 to 20,000 cps. Air recordings were made with a Uher microphone, provided as standard equipment with the recorder, and having the signal fed directly to the recorder operating at a tape speed of 19 cm per second.

The sonagrams (sound spectrograms) were prepared on a Kay Sona-Graph model 662A Sound Spectrograph Analyzer calibrated from 85 to 6000 cps. When the recorded tape speed is reduced by half, and then fed into the analyzer, the response of the latter is doubled to 12,000 cps. The effective filter bandwidths used for the illustrated analyses are indicated in the figure captions, but in each case this value was 300 cycles.

AUDIBLE PULSED SOUNDS IN
THREE SPECIES OF ODONTOCETE CETACEA

Amazon Freshwater Dolphin, Inia geoffrensis (Blainville)

The types of audible pulsed sounds emitted by this species in captivity in 618 minutes of recording and subsequent analysis have recently been described and most of them figured (9: table 1 and figs. 2-9). Ten types of pulsed sounds were deemed sufficiently different to be called by different names. Three of these fell within the category of click trains and in the adults were emitted at times appropriate to a search for environmental information (see 9: fig. 2, for example). These click trains therefore were tentatively adjudged to be echolocation pulses. The young Inia emitted these same sounds, but not necessarily at the precise times when they would have seemed most obviously correlated with a need for environmental information, while the animals failed to emit them on some seemingly proper occasions. This suggested that the use of echolocation involves learning on the part of each individual.

The seven other types of sounds fell into the general category of burst-pulse sounds, but no correlations with behavior could be made. Although Inia was seen to have a variety of sounds, or possibly meaningful intergrades of these sounds, the species was found to be relatively quiet if compared to a highly soniferous species such as Tursiops truncatus.

Additional data acquired since those observations bear out these conclusions.

Recently, two Inia were imported into the United States from near Pucallpa, Peru, to be added to the colony of two males already in residence at Sea World Oceanarium in San Diego, California. The animals were a 200-cm male and a 145-cm female. The two males already at Sea World had been in residence there for 15 months prior to the addition of the two additional animals and consequently were well-established in the pools as their territory. These two animals were about 175 and 185 cm long from snout to caudal-notch.

During a two-hour surface transport period from the Los Angeles airport to the pools at Sea World, the male "screeched" (or "squealed" see 9:15, and fig. 5) three times and the female once. These were the only audible sounds emitted.

Recording was begun just prior to the introduction of the two new animals into the same pool or territory of the two resident males. No unusual behavior and no vocalizations were noted for the following 3 hours. After this period, however, one of the resident males began making an open-mouth threat gesture toward the newly-introduced, but larger, male. The larger (new) male responded in the same way several times. The resident male's aggressiveness was then redirected toward a less formidable opponent -- the small female. The attacks were violent, involving the open-mouth threat gesture, chasing and hard bites or slashes. Several times the female was either knocked or pushed almost clear of the water (Fig. 3). After the attacks, several bleeding wounds were apparent on the

dorsal surfaces of the female and on her flippers and flukes, and we became alarmed at the time that without intervention the small animal might have been killed. She never at any time put up any resistance except flight or attempts to use the large male as a shield. In turn, this animal was never seen to aid the female directly, although he did seem to permit her to attempt to hide behind him. When he did threaten one of the residents, it appeared to be solely in his own behalf.

From the beginning of the attack, and following it, the only audible pulsed sounds were seven soft, very low frequency "squawks" similar to the "barks" shown in Caldwell, et al. (9: fig. 2). These "squawks" were barely audible above the tank noise, even though the pumps had been turned off. Six of the "squawks" occurred during the 35-minute attack episode and the seventh immediately after the net was dropped between the two groups of animals. Following the separation, the attacking resident male continued to show signs of agitation by fast swimming and rapid explosive blowing, but no further sounds were heard in 30 minutes of recording.

Two jaw claps were also produced, similar to, but louder than, the jaw click figured by Caldwell, et al. (9: fig. 9).

Under very similar circumstances in which a large male Tursiops truncatus was introduced into a tank containing four established animals of the same species (two females, one subadult-adult male and one juvenile male), the introduced male was attacked by the dominant female,

a mature cow. While the male received one gash on the top of his head, the attack was not of as severe intensity as the Inia episode described above, and lasted only 10 minutes. However, a minimal count of the phonations was 160. By minimal, we mean that no phonation was counted unless it could be positively identified as a separate, not a continuing, sound and if it could be positively identified from among the other elements of the cacophony. The actual count was probably considerably higher. Details of the sound production in this Tursiops incident are described below under the account for that species.

The rough comparison of number of audible vocalizations under similar circumstances is:

Inia geoffrensis: Four animals in a 36-minute period;
7 pulsed sounds (all "squawks"), or .05 phonations per
animal per minute.

Tursiops truncatus: Five animals in a 10-minute period;
160 pulsed sounds (echolocation bursts, squawks, and pops)
and whistles, or 3.2 phonations per animal per minute.

These figures indicate that, for routine studies of the phonations of captive cetaceans, the primitive Inia is a poorer subject than the more advanced Tursiops, however interesting the comparison may be from a comparative and evolutionary point of view.

Pacific striped dolphin, Lagenorhynchus obliquidens Gill

Two adult females of this species are housed in the delphinid community tank at Marineland of the Pacific. To date, other than the whistle, we have isolated only one sound that is emitted by these animals in an emotional context. This we have called the "tin horn" and seems to be emitted when the animals are excited by any strong stimulus. Fortunately, these animals usually emit bubbles while making this sound so that we can be reasonably certain which animal is making it (Fig. 4).

The "tin horn" is very similar in both animals, but there are constant differences which are quite characteristic and which permit identification of the animal doing the vocalizing. Figure 5 is the typical "tin horn" of one of the animals and Figure 6 is typical of the other. Figure 7 is a sonagram of the "tin horn" emitted in air by the same animal whose in-water "tin horn" is shown in Figure 6. Although the sonagram of the sound emitted in air shows much more detail of the character of the sound than the sonagram of the same sound emitted in water (Fig. 6), the individual similarities are apparent; e.g., the dominant frequency, harmonics, and frequency modulations.

Gales (12:441) figures a pulsed sound emitted by a captive Lagenorhynchus obliquidens that appears to be the same as the one that we are calling a "tin horn." He has called it a "squawk" or "bark." Both of the animals that we had under observation usually emitted this sound as a

couplet. We note that the sounds figured by Gales also appear to be couplets.

It seems reasonable to assume that if we are able to detect by ear individual and characteristic differences in the "tin horn" sounds of each animal, that an animal living in the same environment would also learn to detect them. This species, then, would appear to have "signature" burst-pulse sounds as well as "signature" whistles.

Atlantic bottlenosed dolphin, Tursiops truncatus (Montagu)

Introduction

This well-known species is extremely vocal under natural or semi-natural conditions. Within the audible range the animals emit both pure-tone whistles, click trains associated with object discrimination and environmental exploration, and burst-pulse sounds. Both of the pulsed type sounds are capable of carrying information to other animals.

Our work on the phonations of this species has been conducted mainly on captive but essentially naive animals, as the species is readily conditioned to both the reception and emission of sounds. For comparative purposes, however, we have also worked with animals in training, after training, in isolation, and in groups of two or more. The largest community of animals that we have investigated in captivity consisted of nine animals.

In the following description of the animals, the term "subadult-adult"

will be used. This indicates that, whereas an animal was large enough to be sexually mature and its behavior included copulation, we had no means of knowing if it was capable of producing offspring.

The two principal study sites and subjects were as follows:

1. Marineland of the Pacific, Palos Verdes Peninsula (near Los Angeles), California.

Community tank containing up to seven Tursiops truncatus and two Lagenorhynchus obliquidens. These animals were naive and subject to no training or performance schedules. The colony has not remained stable over the past two years as an overly aggressive mature bull and a subadult-adult female were removed and an adult cow died. In addition to one still-birth, two males have been born into the group since our routine studies of normative behavior began. The total number of communal animals that we have observed and recorded here are one mature bull, three mature cows, two subadult-adult females, one subadult-adult male, and two infant males (one of which now would be classified as a juvenile). The mature bull and one of the cows were also observed and recorded when removed from the community tank and placed in a separate pool for breeding purposes, and one of the subadult-adult females was observed and recorded in isolation.

2. Florida's Gulfarium, Fort Walton Beach, Florida.

Community pool containing up to six animals. These initially included two juvenile males and three mature females. This group was observed and

recorded through capture (June 30, 1964) and transport and daily thereafter for a three-week period. A naive mature bull was added to the group six days later and 13 days later a trained mature bull was added to the group. At this same locality the community tank of show animals was intermittently observed and recorded. This tank contained two adult males and two adult females. In addition, a juvenile male and a juvenile female were recorded daily for a two-week period, both in isolation or separated by a wire-mesh screen.

3. In addition, several Tursiops truncatus were recorded at three other localities for brief periods in order to have a better picture of the individual variations between animals of known sizes and sexes. Histories following capture were made available through the courtesy of the establishments.

- A. Aquarium of Niagara Falls, New York: One subadult-adult female, and one subadult-adult male housed together and trained for performing acts. One subadult-adult male, isolated and naive to training.
- B. Marineland of Florida, St. Augustine, Florida: One subadult-adult female, semi-isolated (separated from several other animals by wire-mesh fence and water courses) and trained for some performing acts.
- C. Marine Biology Facility, United States Naval Station at Pt. Mugu, California: One subadult-adult female, isolated

and naive. Two mature females, each isolated and trained for certain experiments. Two mature males, each isolated and trained for certain experiments.

Many factors influence the quantity and types of phonations in Tursiops truncatus. They are as follows: (1) As the size of the group increases, the number of phonations per animal per hour tends to increase geometrically rather than arithmetically. An increased tempo in vocalization is also reported in chimpanzees when the group size reaches ten or more (13:457). (2) Sound emissions tend to drop out very quickly in isolated animals. Lilly and Miller (16:1874) have also found this to be so. (3) Diurnal periodicity in the number of sound emissions has been demonstrated (21). (4) Stable communities of long duration are less vocal than newly-established communities. (5) There are large individual differences in the "vocalness" of animals. (6) A constant environment without the introduction of stimuli decreases vocalizations. (7) A community tank may suddenly become very vocal for no apparent reason. The unknown stimulus may be internal to the animal but it may also be external and not noted by the observer. For instance, intermittent unexplainable increases in phonations in an uncovered and shallow outdoor community tank in Florida were eventually correlated with the high wind velocities which occur from time to time in the exposed beach area where the tank was located (Fig. 8).

Pulsed Sounds and Concurrent Situations

Sounds emitted prior to and during copulation: The male sex yelp was described, but not figured, by Wood (25). Tavalga and Essapian (24) also reported this same sound during courtship. This sound is the only one in the burst-pulse group that we did not hear in any other context, but it was not by any means a necessary adjunct to the copulatory behavior.

The sex yelp of a mature bull (222 cm in snout to caudal-notch length) during courtship is shown in Figure 9. Figure 10 is the sex yelp of a large (approximately 213 cm in snout to caudal-notch length) but possibly immature male made just prior to erection, and Figure 11 the sex yelp of the same animal just prior to intromission. The sexual yelp of a nine-month-old juvenile is shown in Figure 12. The latter sound was emitted just prior to intromission and copulation with a 226 cm female, his mother. This juvenile male had been under observation since birth, and was noted to have an erection when brushing against the dorsal fin of his mother at the age of two days, to attempt intromission at the age of two weeks and by the age of six weeks had attained a fair degree of efficiency at copulation with the younger female Tursiops and the female Lagenorhynchus in the tank with him since birth. Copulatory activity in this juvenile at 11 months is shown (Fig. 13). Figure 12, however, represents the first time that we were able to identify a recognizable sexual yelp made by this animal. The

ontogeny of the yelp from the more indeterminate but recognizable sound of the juvenile to the fully mature and well-defined yelp of a mature bull appears to be a gradual evolution, rather than a sudden one at sexual maturity. If this is so, the sound should carry information to the female not only regarding the emotional state of the male but also of his maturity and experience.

Sound emitted during play chase: The animals in the community tank at Marineland of the Pacific spend considerable time at play and one of the games principally engaged in is play chasing. When monitoring sounds in the tank, if the observer is looking elsewhere, the occurrence of the typical "chase squawk" (Fig. 14) alerts him that a chase is going on. Frequently, one or both animals will emit bubbles so that identification of the vocalizing animal is simplified. The play chase is not limited to simple fast swimming and sharp turns, but often results in open-mouth encounters between animals. These open-mouth "attacks" (Fig. 15) are often accompanied by considerable emission of echolocation and chase-squawk sounds as well as bubbles from the blowhole and while the attacks seem intense, they do not result in marks and gashes on the recipient animal as do many true fight encounters.

The game of chase is practiced at a very early age by the infants. When a young strays too far from the mother, the mother begins whistling and attempting to herd the infant closer. After the age of four or five

weeks, the infant will frequently try to escape alongside of another animal with which it has been swimming. In the community tank at Marineland the chosen swimming-mate is usually one of the small, agile striped dolphins which can usually out-swim and out-maneuver the Tursiops. The mother may become sufficiently provoked during these episodes to punish the infant, when it is finally caught, by pushing it wiggling and squealing out of the water. The squeal is the normal signature whistle emitted with such intensity that it becomes a squeal.

Sounds emitted during a fight chase: We have not been able to discriminate the squawk emitted during a true fight chase or attack from that emitted during a play chase. A sonagram of a squawk emitted by a dominant cow during a fight chase (Fig. 16) shows only minor differences from the play chase squawk (Fig. 14). This "fight squawk" was emitted after a jaw clap and prior to actual biting. Fights often result in physical injury to the recipient of a bite in the form of scratches and gashes. At times the recipient of an aggressive action may be pinned to the bottom of the tank by one or more dominant animals (Fig. 17).

Sound emitted when lifting or carrying a dead infant: One of the cows at Marineland of the Pacific delivered a stillborn calf after a lingering 3 1/2-hour birth. During this period, we were unable to identify any vocalizations

as originating with the mother and no unusual vocalizations were noted in the recordings. However, for 70 minutes following the birth the mother continued to lift the dead infant to the surface (until it was removed by a diver) and at the same time emitted many low-frequency "squawks."

Although there are several reports of mothers lifting or carrying dead infants (see 8 for a review of this behavior), none mention just how difficult the task is. It was difficult for the mother to lift the dead infant from the floor of the tank as she never used her teeth to grasp it. It was also difficult to get it into a position in which she could maneuver it to the surface. As the dead infant would slip off her snout or melon, this entire procedure was repeated several times before she was successful in carrying it (Fig. 18). Figure 19 is a sonagram of the low-frequency squawks that the mother emitted repeatedly during this lifting and carrying episode.

Whistles and squawks emitted concurrently: There is a definite tendency toward an individually-characteristic pattern when an animal is whistling and squawking at the same time. When a Tursiops truncatus is removed from the water, many "whistle-squawks" are often elicited. The whistles and squawks may be given independently of each other, but when emitted together, the characteristic pattern remains almost constant although the repetition rate of the pulses in the squawk may vary between squawks. Figure 20 is a sonagram of two whistle-squawks of an 11-month-old male

made when the animal was removed from water. Only the low-frequency end of the whistle is shown; it begins to sweep upward at about 4 kHz at 0.1 seconds and 0.9 seconds on the sonagram. Both squawks show a characteristic pattern both between themselves and in temporal relationship to the whistle. Figure 21 is a sonagram of the "whistle-squawk" of a 226-cm female made when the animal was removed from the water. Again only the lower portions of the whistles are shown beginning at about 5 kHz, but again the squawk appears characteristic to the animal and in its temporal relationship to the whistle. Figure 22 is a sonagram of the whistle-squawks of a subadult-adult 203-cm female made when the animal was removed from the water. Again the squawks are almost identical to each other and characteristic of the animal, as well as being constant in the temporal relationship to the whistle contours. The lower frequencies of the whistle contours begin at about 5 kHz. These sounds on all three sonagrams were emitted by animals under circumstances that were almost identical. They had been almost grounded, lifted and placed on a stretcher, and were being weighed and measured. This would lead to the conclusion that this squawk, with its high repetition rate, is emitted when the animal is strongly protesting, and also that it is characteristic to each individual animal. We have, however, recorded one animal that never whistled in water without squawking (Fig. 23) for over a three-week period. This was a mature bull (222 cm long), a very dominant animal. He was recorded under a wide variety of conditions which included stranding on the bottom

of his pool, isolation, introduction of novel sounds and objects, and courtship. This whistle-type phonation did not vary. As this is the only animal that we recorded characterized by a whistle-squawk rather than a whistle, no generalization can be made.

Sounds emitted while performing a difficult task: The Tursiops truncatus in the community tank have a characteristic soft mewling sound emitted when attempting to pick up small objects such as pebbles or coins. A nine-month-old male was heard emitting this sound (Fig. 24) when ferreting a small rock out of a crevice (Fig. 25), indicating that the ability to emit the extremely fast pulses that we associate with a fine discrimination is present at least by this age. We found it surprising that this same fine discrimination sound is also consistently emitted when the animal is performing a difficult maneuvering task. In the Marineland of the Pacific community tank a tether-ball was attached to a line which in turn was fixed to the floor of the tank. A sport was developed by the animals in which the objective was to push the ball (which contained enough air to cause it to put a strain on the line holding it when it tried to float to the surface) forward by pushing it with the snout until the ball touched the bottom of the tank (Fig. 26). This was a difficult task since the ball would immediately spring back to the vertical position at the end of its restraining line if it became the slightest bit off center on the snout tip of the animal pushing it. Rapidly pulsed mewling sounds always accompanied this task. This is a slightly different use of what appears to be echolocation from that of

discriminating size or texture and is an indication of the possible extent of the use of echolocation in this species. This task would be performed in other animals on the basis of cues supplied to the kinesthetic and tactile senses. It seems reasonable to assume that other animals in the community would learn to associate this mewling sound with a harmless object in the vicinity, and would be attracted to the sound source out of curiosity.

Sounds emitted when feeding: The observation windows at Marineland of the Pacific permit good underwater vision into the tank but do not allow the observer to see what is going on above the surface of the water. We are always alerted that a surface feeding has begun, however, by the medley of characteristic echolocation sounds of the animals. These sounds vary from loud, more slowly pulsed echolocation clicks to the mewling used in making fine discriminations. Some of them are almost identical to the feeding sounds in Phocaena phocaena (4: fig. 45) or the fine discrimination shown for Tursiops in this paper (Fig. 24). Other sounds emitted in this context are louder and more slowly pulsed similar to the pulses shown in the first section of Fig. 27. It would be unlikely that individual members of a Tursiops captive community or wild school did not learn to identify these sounds. In the wild these would serve as a cue that a fish school had been encountered.

Sounds emitted in self-conflict situations: On one occasion, a mature bull

emitted "cracks" when placed in a severe conflict situation (Fig. 27). We were attempting to entice the animal through a narrow gate in a figure-eight-shaped pool (Fig. 8) by offering fish just across the gate from the side in which he was housed. This species is notoriously afraid of narrow spaces and the animal was placed in severe self-conflict even though he had been in captivity most of his life and was very familiar with the captive environment. The sonagram (Fig. 27) shows a typical segment of the phonations at the time. Loud echolocation clicks followed by the rapid clicks associated with fine discrimination are in turn followed by two loud cracks. After an initial exposure to the situation, the intensity of the behavior and phonations decreased to some degree and loud squawks and barks were emitted (Fig. 28).

Sound emitted when new animal was introduced into pool with other animals: When a large bull was introduced into a pool with an established colony, a sound was recorded which we have not heard in this species on any other occasion. This was a puppy-like "whimper" (Fig. 29). Collias (11:387) has noted a similarity in the emotional sounds emitted by different species even when the sounds are produced by different parts of the anatomy. Because of the seemingly infantile nature of this sound, it is tempting to speculate that it is one of appeasement. There were several animals in the tank at the time, however, and we were unable to identify the specific source of the sound.

Sounds emitted in reaction to novel stimuli: Fear is easily elicited in

this species by the introduction of any strange object (6, 17). Captive Tursiops truncatus show a fairly constant pattern in their reaction to novel stimuli. When the object is first introduced, "cracks" (10) or "pops" may be momentarily elicited. The "pop" is basically the same sound as a "crack," but of lower intensity. In our work these sounds have usually been associated with a startle reaction and sudden flight. Figure 30 shows two naive Tursiops truncatus fleeing from a dumbbell that has just been lowered in a fixed position into the center of their pool. Figures 31 and 32 are sonagrams of a crack and a pop emitted at this time. On the other hand, Lilly (15) has interpreted as a threat signal what appears, from his verbal description, to be the same sound as our crack.

After the momentary emission of the preceding sounds, the animals become very quiet, emitting only an occasional "chirp." This is a brief pure tone emission, frequently but not always with an abrupt upward frequency modulation. We have not been classifying it as a whistle.

After this period of almost intense silence, sounds of soft echolocation occur, which may progress to "squeaks" or high-pitched barks. Figures 33, 34 and 35 are sonagrams of the "squeaks" or high-pitched barks which began after a 30-minute period of comparative silence following the introduction of the dumbbell. Some of the sounds (Fig. 35) had a more bird-like or squeaky quality than others (Figs. 33 and 34). We do not know whether this difference is in sounds emitted in a slightly different emotional context or whether it is the same basic sound but produced by a different

animal. The tank contained four animals of assorted sizes and sexes and we do not know which animal or animals might have been emitting the barks.

Very similar but soft "barks" (Fig. 36) were emitted after a model dolphin was introduced to these same four naive animals (Fig. 37).

On still another occasion, when a strange bull was introduced into this pool, similar "squeaks" and "barks" were again emitted (Figs. 38 and 39).

Marler (18: 582f.) has called attention to the frequency of the term "bark" when used to describe animal sounds emitted in a situation of danger. This has been reported previously for such widely varying groups as primates and ungulates.

Absence of pulsed sounds: This species will occasionally become completely silent, even in the wild and in groups of ten or more. Before a quiescent period, the sounds taper off gradually and include no high intensity vocalizations. Conversely an abrupt cessation of all sound emissions is common to captures made in the wild and certain captive situations in which the source of potential danger can be seen coming or when any strange or frightening stimulus is introduced. Such an abrupt cessation of sound doubtless is as meaningful an alarm signal as a specific vocalization.

Signature in the pulsed sounds: There is a good possibility that individuals

of this species have pulsed sounds that are characteristic to the animal. Backus and Schevill (1: 514f) have shown this for the sperm whale, Physeter catodon, and the Pacific striped dolphins mentioned above have characteristic burst-pulse sounds. The Tursiops protest "whistle-squawks" referred to above appear characteristic, as do the "sex yelps."

SUMMARY AND CONCLUSIONS

For purposes of a study of communication in odontocete Cetacea, captive Inia geoffrensis show less promise than Tursiops truncatus. This is particularly so in sound communication because of the infrequent vocalizations of the former species.

It seems theoretically probable that when the ancestors of Cetacea entered the aquatic environment they either brought with them, or developed, pulsed sounds that were useful in communicating the emotional state of the individual. From these might have developed their use in obtaining environmental information by echolocation. The original use of these sounds would still be retained, however. It would seem that the more social species almost necessarily would have developed a greater repertoire of sound and a tendency to use it more frequently. A few of the many pulsed sounds emitted by Tursiops truncatus have been correlated with concurrent behaviors and presented here; others are present but are

omitted because of their infrequency and a sufficient number of behavioral correlations. In an animal as playful as Tursiops, the possibility of their playing with the vocalizations should not be overlooked, particularly in the juveniles. Also some individuals of this species are natural mimics and we do not discount the possibility of vocal mimicry if the sound is within the physical capabilities of the animal.

In general, we have found that community tank studies offer the best opportunity for a correlation of sound production and social behavior in captive Cetacea. The greater the number of animals the more sound production per animal. In our experience, vocalizations are greatly reduced by the two factors of length of time in captivity and reduction of number of animals contained together. In our work (5) with the spotted dolphin, Stenella plagiodon (Cope), we recorded two females, captive only a month, for several days before we obtained whistles and these were finally elicited only by lowering the water and grounding the animals. This is in sharp contrast to the medley of whistles (or squeals) recorded in the wild by Schevill and Watkins (23), and points up the need for extreme caution in making speculations or conclusions regarding the behavior and phonations of any species of animal in the wild based only on observations and recordings of captives.

At present, our only completely reliable method for identifying a community animal's vocalizations is to place the individual in isolation for a day or two, record, and then return it to the community tank. When we

are working with other people's animals, this frequently cannot be done. Therefore the greatest contribution to this type of work that we can envision that might come out of this meeting is some form of sound transmission device whereby a vocalization could be definitely attributed to a specific individual. We have been able to identify whistles of individual animals in a Tursiops community tank studies only after days or weeks of observations and tape analysis. This is extremely slow work, however, with no guarantee of results. If instrumentation could be devised to pinpoint the sound source, the work on both whistles and pulsed sounds could be speeded up enormously.

ACKNOWLEDGMENTS

Access to the captive Tursiops and Lagenorhynchus whose behavior is reported on herein was made primarily through the generous cooperation of John H. Prescott, Curator at Marineland of the Pacific near Los Angeles, California, and David H. Brown, formerly Curator of Mammals at that establishment. Additional Tursiops were studied in detail with the helpful assistance of J. B. Siebenaler, General Manager of Florida's Gulfarium, Fort Walton Beach. Other Tursiops were studied in lesser detail at Marineland of Florida with the cooperation of C. F. "Cliff" Townsend; at the Aquarium of Niagara Falls, New York, with the help of Winfield H. Brady; and at the United States Navy Marine Biology Facility at Pt. Mugu,

California, with the assistance of F.G. Wood, William E. Evans and Bill A. Powell. New and recent studies of Inia behavior discussed herein were accomplished with the enthusiastic support of Kent Burgess, Director of Training at Sea World, San Diego, California. In addition, much of the work at all of these establishments could not have been done without the interested but unheralded help and cooperation received from the large support staffs at all of the study sites.

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This paper constitutes contribution number 26 from the Marineland of the Pacific Research Laboratory, Los Angeles, California, and a contribution from the research programs of Florida's Gulfarium, Fort Walton Beach, and Sea World Oceanarium, San Diego, California.



Fig. 1. Captive Tursiops truncatus: Precopulatory behavior in which a subadult-adult male (on left) and an adult female (upside-down on right) have swum rapidly toward one another and violently bumped melons. This behavior is usually accompanied by the underwater release of large numbers of small air bubbles and the production of loud vocalizations we are calling "squawks."



Fig. 2. Captive Tursiops truncatus: Adult female (right) holding down her juvenile male calf in a situation in which she appeared to be punishing him for continually annoying her.



Fig. 3. Captive Inia geoffrensis: Newly-introduced small female being knocked almost out of the water by the force of an aggressive action by a larger resident male.



Fig. 4. Captive Lagenorhynchus obliquidens: Adult-sized female releasing bubbles during production of sound we are calling "tin horn." (See Fig. 5 for such sounds produced by this animal, and Figs. 6 and 7 for such sounds produced by another female).

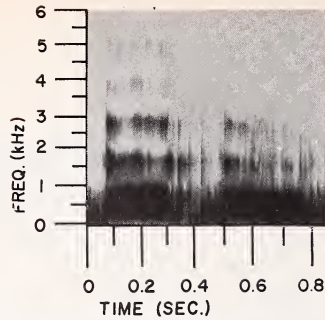


Fig. 5. Captive Lagenorhynchus obliquidens: Sonagram of sounds we are calling "tin horn" produced in water by a female of adult size (Fig. 4). (Effective filter bandwidth 300 cycles)

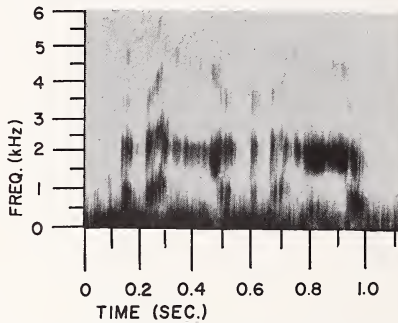


Fig. 6. Captive Lagenorhynchus obliquidens: Sonagram of sounds we are calling "tin horn" produced in water by a female of adult size other than the one producing the sound shown in Fig. 5. (Effective filter bandwidth 300 cycles)

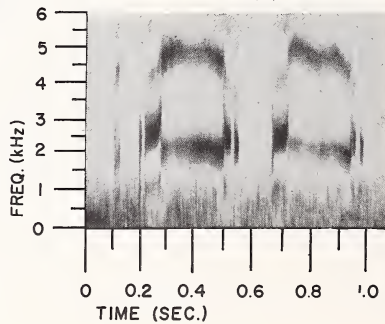


Fig. 7. Captive Lagenorhynchus obliquidens: Sonagram of sounds we are calling "tin horn" produced out of water by the female of adult size which produces the sound shown in Fig. 6. (Effective filter bandwidth 300 cycles)



Fig. 8. Study site at Florida's Gulfarium showing constriction between pools which posed a conflict situation for Tursiops truncatus being enticed between pools.

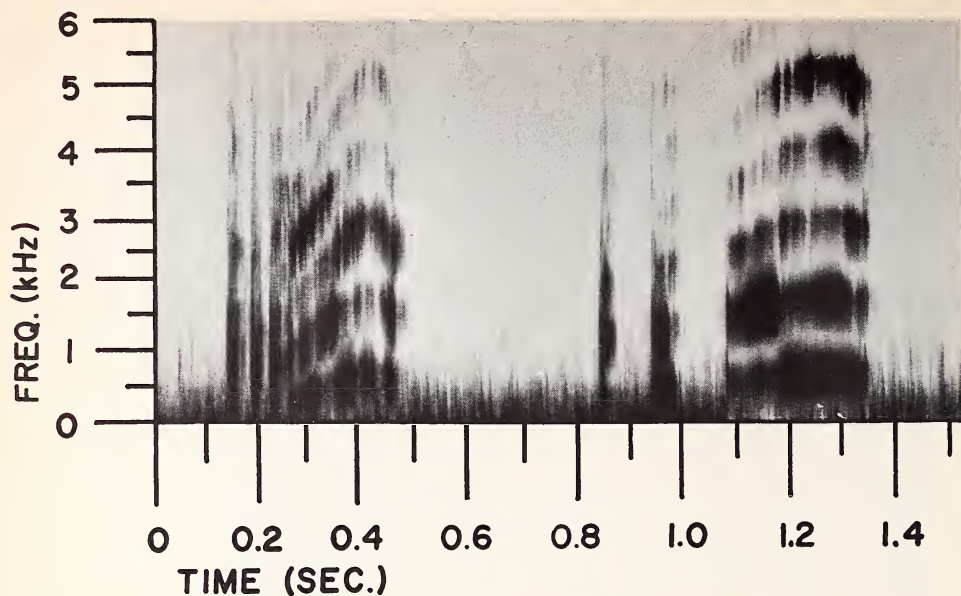


Fig. 9. Captive Tursiops truncatus: Sonagram of sounds termed "sex yelp" produced by an adult male while making apparent sexual advances toward an adult female. (Effective filter bandwidth 300 cycles)

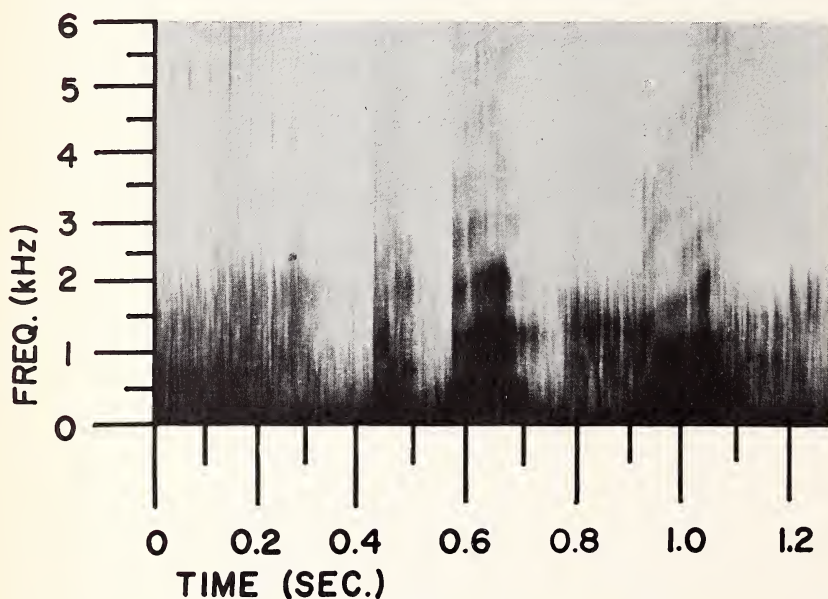


Fig. 10. Captive Tursiops truncatus: Sonagram of sounds termed "sex yelp" produced by a subadult-adult male just prior to erection of penis. (Effective filter bandwidth 300 cycles)

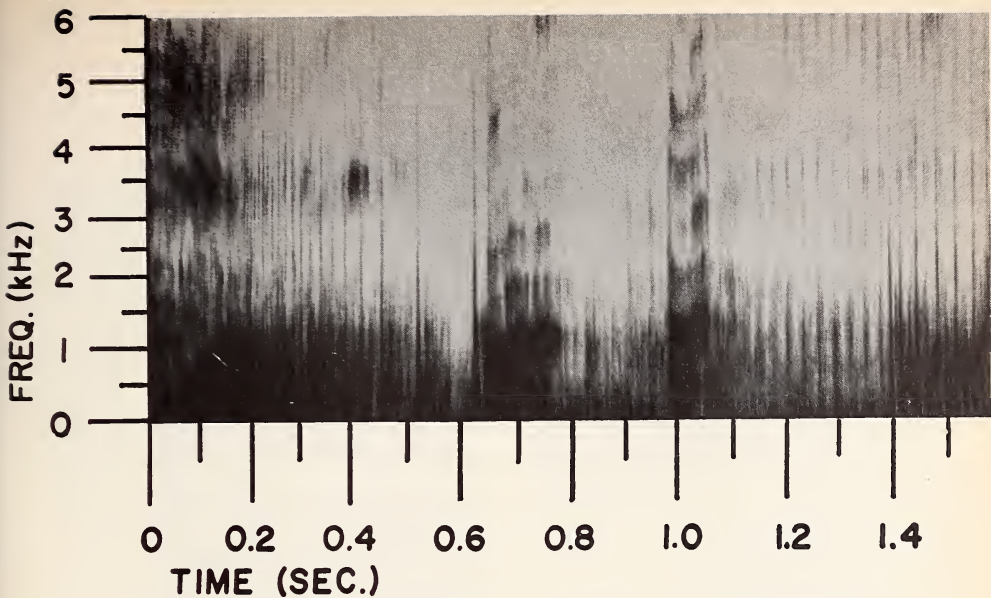


Fig. 11. Captive Tursiops truncatus: Sonagram of sounds termed "sex yelp" produced by a subadult-adult male just prior to intromission with a subadult-adult female. (Effective filter bandwidth 300 cycles)

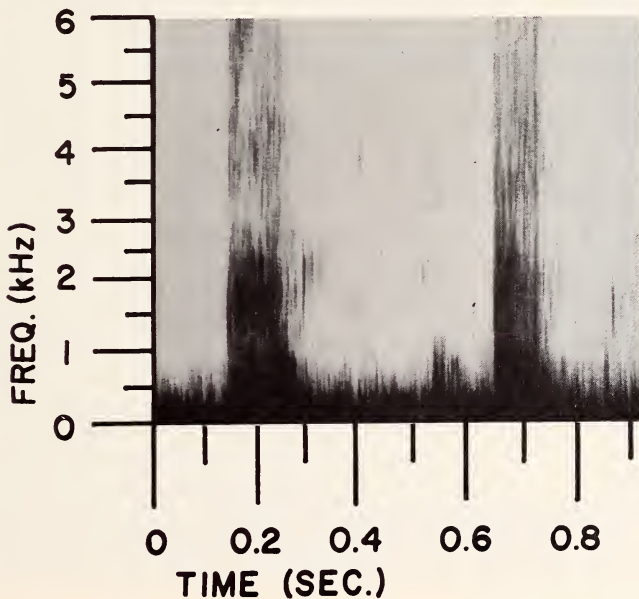


Fig. 12. Captive Tursiops truncatus: Sonagram of sounds termed "sex yelp" produced by a nine-month-old juvenile male just prior to intromission with his mother. (Effective filter bandwidth 300 cycles)



Fig. 13. Captive Tursiops truncatus: Juvenile male (lower) attempting intromission with his mother. This behavior is often immediately preceded by the production of "sex yelp" sound by the male. (See Fig. 12)

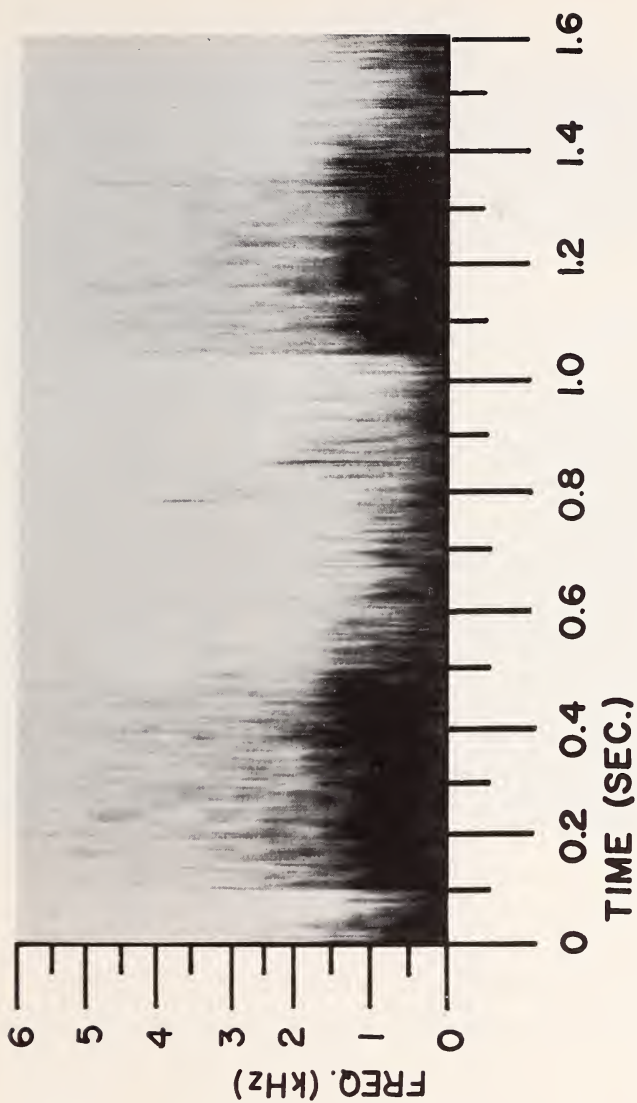


Fig. 14. Captive Tursiops truncatus: Sonagram of sounds we are calling "chase squawks" produced during a play chase between an adult female and her juvenile male calf. See Fig. 15 for concurrent behavior. (Effective filter bandwidth 300 cycles)



Fig. 15. Captive Tursiops truncatus: Play chase, in which an adult female (left) here "mouths," without injuring him, her juvenile male calf. This behavior, often accompanied by loud sounds termed "chase squawks," frequently includes the underwater release of streams of small bubbles of air. (See Fig. 14)

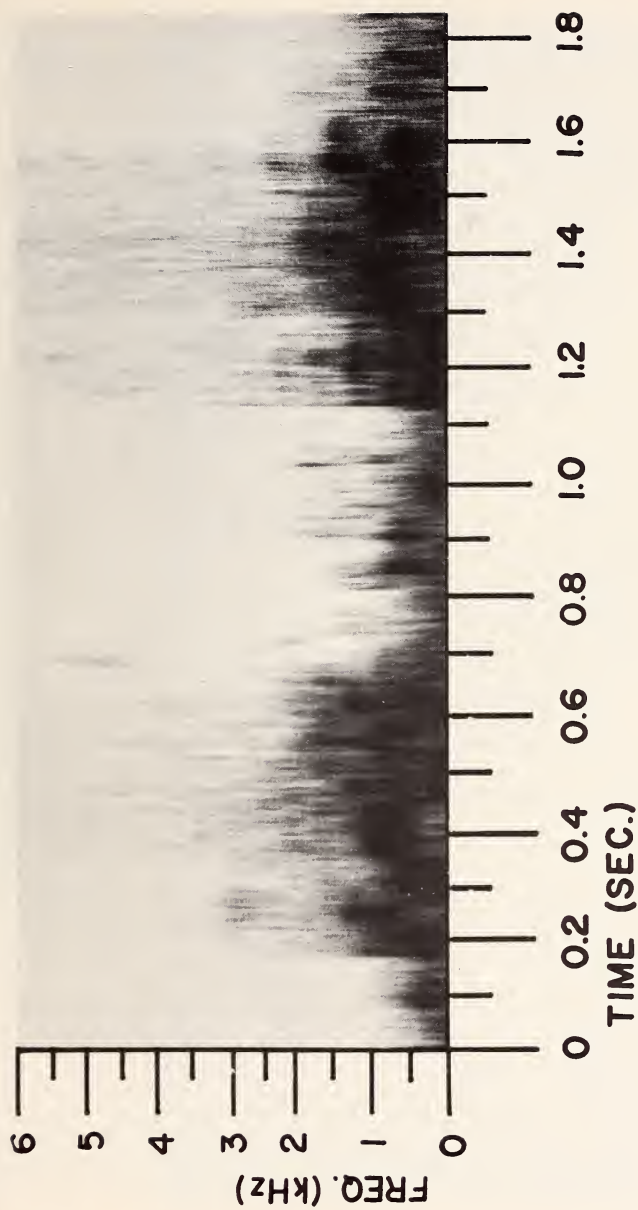


Fig. 16. Captive Tursiops truncatus: Sonagram of sounds produced during a fight between an adult female and a subadult-adult male, and termed "fight squawks." (Effective filter bandwidth 300 cycles)



Fig. 17. Captive Tursiops truncatus: Fight, in which two females (an adult and a subadult-adult) have pinned a subadult-adult male to the floor of the tank. This behavior, often accompanied by loud sounds termed "fight squawks," frequently results in scratches and gashes on the skin of the recipient of the action. (See Fig. 16)



Fig. 18. Captive Tursiops truncatus: Adult female carrying her still-born young over her melon. This behavior was accompanied by repeated vocalizations, of the type shown in Fig. 19, until after the dead calf was removed from the tank.

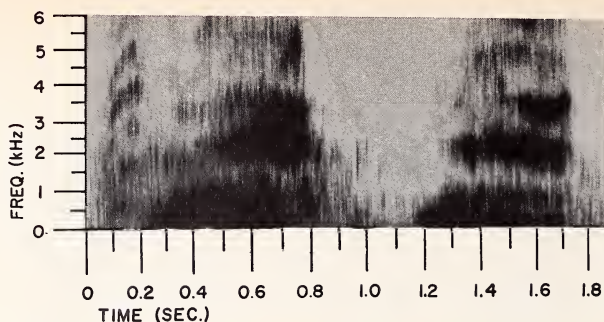


Fig. 19. Captive Tursiops truncatus: Sonagram of sounds produced by adult female carrying her dead stillborn calf. See Fig. 18 for concurrent behavior. (Effective filter bandwidth 300 cycles)

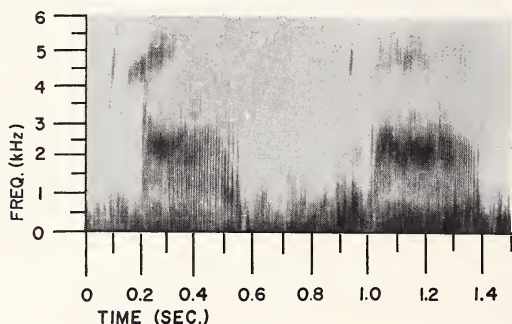


Fig. 20. Captive Tursiops truncatus. Sonagram of sounds termed "whistle-squawks" produced out of water by juvenile male. (Effective filter bandwidth 300 cycles)

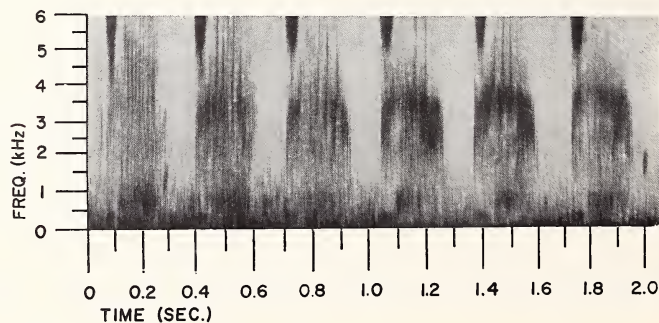


Fig. 21. Captive Tursiops truncatus: Sonagram of sounds termed "whistle-squawks" produced out of water by adult female. (Effective filter bandwidth 300 cycles)

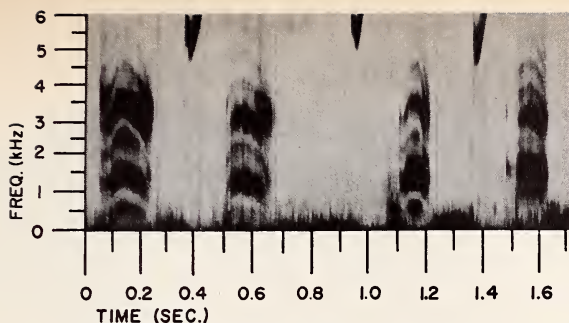


Fig. 22. Captive Tursiops truncatus: Sonagram of sounds termed "whistle-squawks" produced out of water by subadult-adult female. (Effective filter bandwidth 300 cycles)

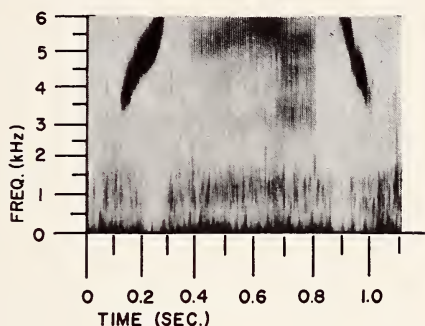


Fig. 23. Captive Tursiops truncatus: Sonagram of sound termed "whistle-squawk" produced in water by adult male. (Effective filter bandwidth 300 cycles)

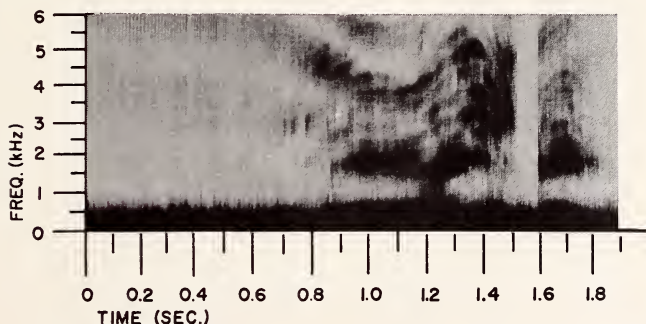


Fig. 24. Captive Tursiops truncatus: Sonagram of fine-discrimination echolocation clicks produced by juvenile male in search of tiny rock in crevice on bottom of tank. See Fig. 25 for concurrent behavior. (Effective filter bandwidth 300 cycles)



Fig. 25. Captive Tursiops truncatus: Juvenile male attempting to pick up tiny rock in crevice on tank bottom, the activity accompanied by the production of the fine-discrimination echolocation clicks as shown in

Fig. 24.



Fig. 26. Captive Tursiops truncatus: Juvenile male pushing tether-ball toward the bottom of his tank; the activity is accompanied by the production of fine-discrimination echolocation clicks similar to those shown in

Fig. 24.

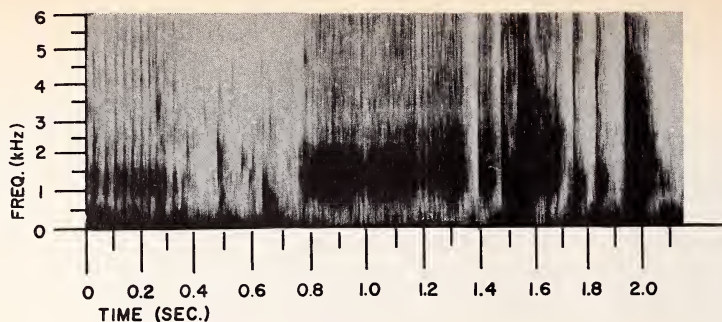


Fig. 27. Captive Tursiops truncatus: Sonogram of sounds first produced by adult male in self-conflict situation in which he had to choose between passing through a narrow gateway (Fig. 8) or losing a fish reward on the other side. Sounds are echolocation clicks and phonation termed "cracks." The echolocation clicks extend to 1.5 seconds. A crack occurs at 1.55 and another at 1.95 seconds.

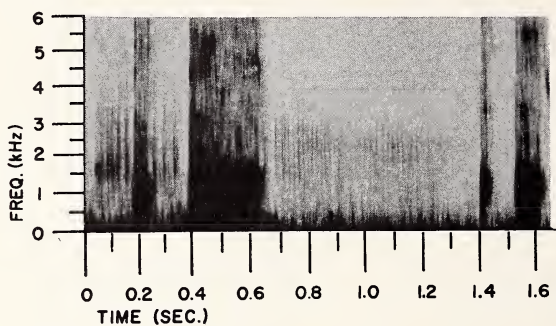


Fig. 28. Captive Tursiops truncatus: Sonogram of sounds termed "squawks" produced by adult male in the same self-conflict situation described in Fig. 27. (Effective filter bandwidth 300 cycles)

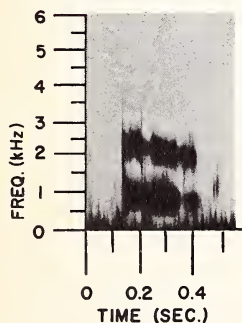


Fig. 29. Captive Tursiops truncatus: Sonogram of sound termed "whimper" produced when adult male was introduced into a tank with four newly-captured animals (two adult females, one subadult-adult male, one young female). (Effective filter bandwidth 300 cycles)



Fig. 30. Captive Tursiops truncatus: Two naive animals avoiding a dumbbell suspended in a fixed location in the center of their pool. This situation first resulted in the production of sounds termed "cracks" and "pops," later followed by "squeaks," "barks" and "soft barks" after a period of silence. (See Figs. 31, 32, 33, 34, and 35)

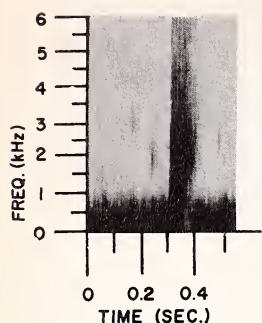


Fig. 31. Captive Tursiops truncatus: Sonagram of very loud sound termed a "crack," produced under the same conditions and during the same sequence with the dumbbell shown in Fig. 30. (Effective filter bandwidth 300 cycles)

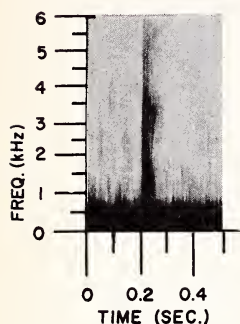


Fig. 32. Captive Tursiops truncatus: Sonagram of loud sound termed a "pop," produced under the same conditions and during the same sequence with the dumbbell shown in Fig. 30. (Effective filter bandwidth 300 cycles)

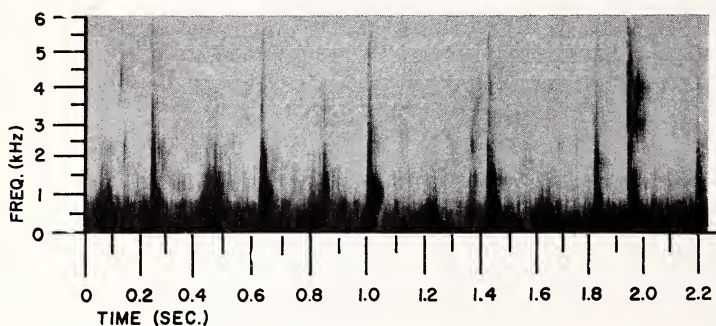


Fig. 33. Captive Tursiops truncatus: Sonagram of sounds, termed "squeaks" or high-pitched barks, produced when a dumbbell was first suspended over the center of a pool containing four newly-captured animals (two adult females, one subadult-adult male, one young male). See Fig. 30 for concurrent behavior. (Effective filter bandwidth 300 cycles)

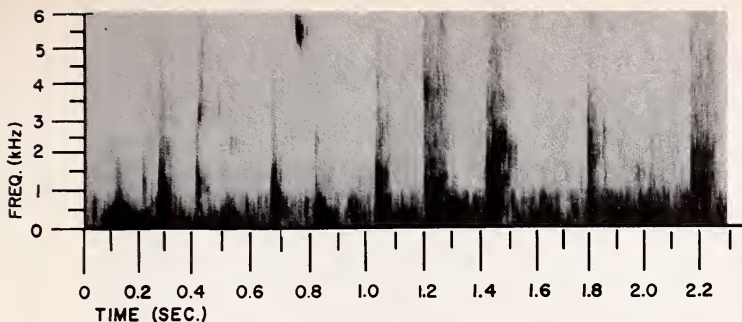


Fig. 34. Captive Tursiops truncatus: Sonagram of sounds, termed "squeaks" or high-pitched "barks," produced under the same conditions and during the same sequence with the dumbbell shown in Fig. 30. (Effective filter bandwidth 300 cycles)

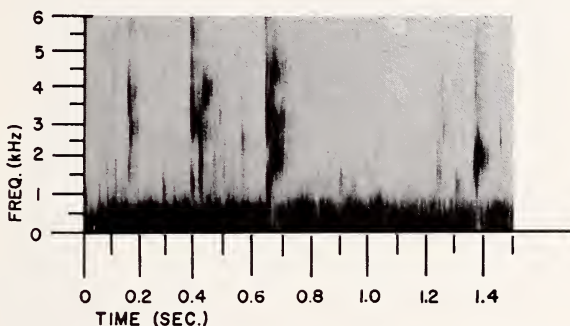


Fig. 35. Captive Tursiops truncatus: Sonagram of sounds termed "squeaks" or high-pitched "barks," produced under the same conditions and during the same sequence with the dumbbell shown in Fig. 30. (Effective filter bandwidth 300 cycles)

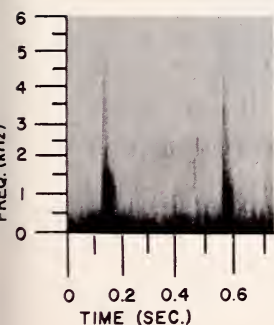


Fig. 36. Captive Tursiops truncatus: Sonagram of sounds termed "soft barks," produced when a model of a small dolphin was first floated into a tank containing four newly-captured animals (two adult females, one subadult-adult male, one young female). See Fig. 37. (Effective filter bandwidth 300 cycles)

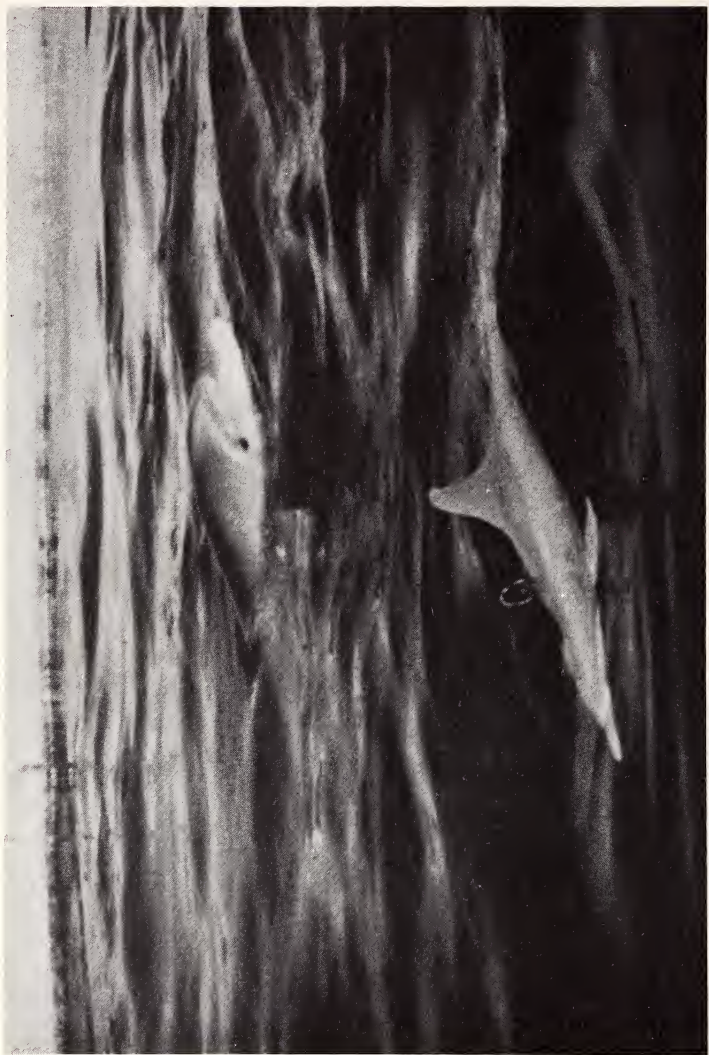


Fig. 37. Captive Tursiops truncatus: Naive animal avoiding a small model dolphin floating in the center of its pool. This situation resulted in the production of sounds termed soft "barks." (See Fig. 36)

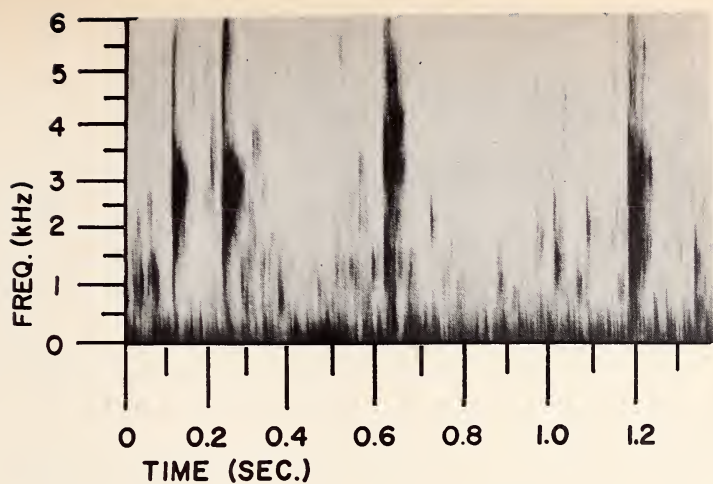


Fig. 38. Captive Tursiops truncatus: Sonagram of sounds termed "squeaks" produced when a mature male was introduced into a tank with four newly-captured animals (two adult females, one subadult-adult male, one young male). (Effective filter bandwidth 300 cycles)

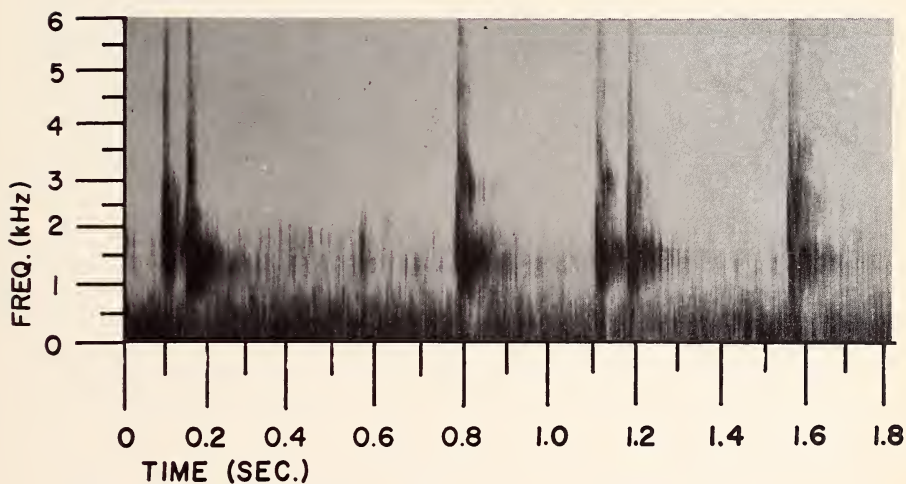


Fig. 39. Captive Tursiops truncatus: Sonagram of sounds termed "squeaks" produced under the same conditions and during the same sequence as those shown in Fig. 38. (Effective filter bandwidth 300 cycles)

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ABSTRACT:

Intraspecific transfer of information by means of audible pulsed sounds is compared in two widely divergent species of Cetacea; namely, the primitive Amazon fresh-water dolphin (Inia geoffrensis) and the more recently evolved and highly social Atlantic bottlenosed dolphin (Tursiops truncatus).

Inia has been found to emit pulsed sounds, some of which are probably used in an emotional context and others in echolocation. How-

ever, the sounds of Inia are infrequently used in captivity, and are faint and of low frequency. Results of attempted behavioral correlates with sound other than echolocation in Inia have been meager. No pure-tone whistles have been recorded from this species.

Tursiops is more vocal in both number and variety of pulsed sounds. Eleven of these varieties are described and figured in sonagrams, and the situations which elicited them are presented. Only one of these sounds, the "sex yelp," is entirely specific. The others are capable of relaying a more general but basic type of information such as "flee" or "approach" or "hold still." The recipient may then obtain more specific information by further investigations of his own.

The importance of the total context of the situation under which a sound is received is emphasized. The particular importance of the pure-tone whistle emission to the total auditory input at the perceptual level is delineated.

It is postulated that many of the burst-pulse sounds are characteristic of the individual producing them and can be recognized by other individuals in identification of the emitter. Some evidence for this postulate is presented.

Brief mention is made of a pulsed sound emission of the Pacific striped dolphin (Lagenorhynchus obliquidens), a species intermediate between the two extremes on which most of the work reported on was conducted.

DISCUSSION

par

J. C. LEVY

Cette note ne fait état que de renseignements quantitatifs, il y a donc peu de matière à discussion pour un physicien.

Toutefois, il est intéressant de rapprocher cette communication de celle du Dr. Jarvis Bastian car toutes deux concernent les moyens de communications entre animaux.

La communication du Dr. Bastian fait état d'expériences menées dans un cas précis. A la suite d'un entraînement, lui même assez compliqué, les animaux sont placés dans un cas simple et n'ont qu'à se communiquer un digit d'information à chaque expérience. Des observations et statistiques précises ont pu être faites.

La communication du Dr. Caldwell correspond à des observations relatives aux communications sociales entre animaux et le contenu des messages à transmettre est bien moins connu a priori.

Nous ne pouvons en saisir que le sens général: appétit sexuel, faim, danger ... mais ce que nous ne pouvons pas encore savoir, c'est si ces messages comportent des nuances analogues à notre langage permettant à chaque individu d'exprimer un certain nombre d'idées. Je pense qu'il faudrait pour cela imaginer des expériences reproduisant des situations sociales réelles de façon à pouvoir effectuer des observations systématiques. Je me contente d'émettre cette idée, je ne sais pas encore comment il serait possible de la réaliser.

Par exemple, un animal signale la présence du danger, peut-il faire comprendre à ses congénères la nature de ce danger, son imminence, indiquer ce qu'il faut faire pour y échapper?

Je terminerai par une remarque relative à la différence constatée par le Dr. Caldwell entre le "Tursiops" et l'"Inia".

Les signaux de communication sociale de l'Inia sont de même nature que les "Clicks" d'écholocation. Cela confirme l'hypothèse portée par le Dr. Bastian, qui suppose que les signaux émis par un dauphin à l'usage d'un autre sont composés par les "Clicks" lui servant à s'orienter, et qui par la même occasion peuvent servir à orienter un congénère.

Cela pose encore un nouveau problème: des dauphins d'une même espèce peuvent communiquer entre eux, en est-il de même de dauphins d'espèces différentes. Cela pose ainsi le problème de la communication entre l'homme et l'animal, qui seule nous permettrait de bien comprendre ce dernier.

COMMUNICATIVE CHARACTERS OF SONAR SIGNALS IN BATS

by

F. P. MOHRES

Progress in experimental research often depends upon a useful working hypothesis. This consists of simplification of a problem emphasizing certain aspects at the cost of others. With this method we may hope to obtain an integral view of our research. In studying the problems of sonar systems in animals one simplification we may make is to separate sonar signals and communication signals.

Most animal sounds are produced as a means of inter-individual communication. Acoustic signals used in animal sonar systems serve for object detection and identification, but, of course, this does not exclude the possibility that they are used for communicative purposes too. Up to the present time the problem of the communicative content of sonar signals has not attracted much attention. This is true even in the case of bats in which sonar systems have been thoroughly studied. My contribution to this subject should serve as a stimulus for further studies rather than as an ex-
lophidae family, and is based on personal observations and experiments, most of them hitherto unpublished.

For years we have been keeping different species of bats in captivity in our laboratory in living conditions as close to nature as possible. These bats are usually kept in small or large groups, and are trained to return on their own to their sleeping cage which they regard as "home". The bats have to fetch their food from the experimenter's hand while they are in flight. After a short phase of adjustment the bats behave quite normally and offer opportunities for observation and experimentation which would not be possible in field-studies. All the results presented below have been drawn from experiments with these laboratory-colonies of bats. As far as possible they have been checked by observations of free-living colonies.

Individual recognition within the group by means of sonar signals

Bats are social animals living in small or large groups. In our laboratory-colonies these groups showed a social structure with well-defined and rather stable ranks. In watching a small group it was observed that all members of that group knew each other individually. This was definitely confirmed in some long-term studies done on a group of Rhinolophus equinum (Schreb.) (bigger European Horseshoe bats). Each bat was marked with a colored tag, and the group was gradually augmented from two members to ten members. The first two members of the group proved to be more attached to each other than to the other bats which joined the group later. Grouping at resting places after flight revealed special and rather stable preferences between certain individuals. The small groups which met before the final crowding of the whole group generally consisted of the same individuals. Since the factor of preference for the same locality may be excluded, this means that the bats must have been able to identify their groupmates. The question, of course, arose as to how the bats managed to recognize each other. As vision and olfaction in horseshoe bats are very poorly developed, it seemed most likely there was some kind of acoustical identification. However, in considering this possibility it was noted that the repertory of communication sounds in horseshoe bats is extremely limited, and does not contain an attracting signal. Further experimentation finally revealed that these bats identified each other by their different orientation signals. Thus, the signals serve as both sonar and communication signals.

Experiments were performed in the following manner. A group of horseshoe bats was transferred with the "home" cage to a big room in which they had never been before. The new flight room offered many adequate resting places. The bats were called to get their food in a small adjacent feeding

room which was separated from the main room by a door opened at feeding time. After a fortnight the bats chose definite resting places where they chewed the insects given to them and cleaned their fur and wings before returning to the "home" cage. These resting places were then fitted with cardboard screens which were fixed so that the resting place was accessible only from below to the bats in flight, and so that the bat hanging behind the screen was totally hidden and invisible from the room. After being fed in the feeding room the bats were allowed to return singly to the main room. If the first bat had chosen its resting place, the next one was admitted, and so on. The bats arriving later had no difficulty in finding their hidden companions, even when the hiding places of the firstcomers were continuously changed. (We chased them to another place when they came back to the same place they had occupied in the preceeding experiment.) Careful observation revealed that the hidden bats produced no sounds other than their normal orientation signals. As optical and olfactory recognition could be excluded, we thought the bats might have recognized each other by the pitch difference in their sonar signals. It was tempting to think of replacing the living bats hiding behind the screen by a loud-speaker, but unfortunately, this was not feasible. Bats do not respond to a loud-speaker transmitting orientation signals because there is inevitable signal distortion and because there are directional character differences in sound emission between a loud-speaker and another bat.

To obtain a valid answer to this question a different experimental arrangement was used. One wall of the main room was covered with a big cloth curtain hanging from the ceiling to the floor at a distance of 40 cm from the wall. On the wall a number of small boxes were fixed in different positions. Each box had a front door consisting of a

wooden frame covered with plastic wire netting. At the beginning of each experiment the curtain was drawn aside. The first bat returning from the feeding room was gently taken from its resting place and put in one of the boxes mentioned above. After the front door of the box had been closed, the cloth curtain was drawn over the wall carefully so that wall and boxes were totally hidden. The next bats returning to the main room after some circle-flights, usually landed on the curtain just at the spot behind which the first bat was hidden. If the hidden bat did not emit orientation sounds, the newcomers did not find it. In some cases it was necessary to stimulate the bat by tongue-clicking, after which it began to produce orientation signals and was immediately found by its groupmates.

In this experimental situation the hidden bat could only have been detected by acoustical means. Detection and identification of the hidden bat by echolocation can be excluded because of the scattering produced by the dense cloth of the curtain. The only possible explanation of the observed behaviour is that orientation sounds in horseshoe bats also serve as communication sounds, which in this special case were assembling calls. It is evident that these bats were able to distinguish the signals of individual bats. As far as we can tell, this can only be explained by frequency discrimination. The orientation signals of horseshoe bats are composed of high tones having a very constant frequency. The frequency is characteristic for the species and varies from individual to individual over a range of 1 to 1,5 kHz (MÓHRES 1953).

Alarm effect of orientation signals

There is strong evidence that orientation sounds can also act as alarm signals. In visiting colonies of free-living bats it has often been

observed that the sudden start of one disturbed animal is immediately followed by a general take-off of the whole group. One starting bat can thus release the flight of a thousand or more bats. As far as we can judge from our present knowledge no special alarm calls or alarm signals are involved in this group reaction. It seems that the speed-related transformations of the pattern of orientation signals act as a releaser.

This explanation may be regarded as proven for horseshoe bats. In this species the reaction to Doppler shift caused by movement is very conspicuous. If one bat starts with high acceleration, the other bats hear its orientation tones which have a very steep frequency decline. A signal pattern of this kind picked up with a microphone and transmitted to a group of horseshoe bats in another room causes high excitation, and often hasty escape. Similar experiments done on other species of bats would be very interesting.

Orientation signals as threatening calls

We have a few indications that orientation signals can act as threatening calls. When a group of Asellia tridens (Hipposideridae) and Rhinolophus acrotis (Rhinolophidae) were kept in the same laboratory, the two species used to hang separately. If a flying Asellia approached a hanging Rhinolophus, the latter emitted a short, hastily-uttered series of orientation sound. In all cases this caused the Asellia to immediately change flight direction and turn away. Rhinolophus was never observed to utter a special threatening sound in this situation. A fighting shriek was uttered only in close fight.

Orientation signals as guidance signals

As has already been described by MÖHRES (1953 b) orientation sounds can

serve as guidance signals to secure contact between the mother-bat and her young during the first flights of the latter. Control of the sound production of the mother and her young showed that the young immediately lost contact with the mother during the intervals between her signal emissions. Landing at the nearest possible spot and pouring forth rhythmical distress calls, the young alarmed the mother and caused her to return and reestablish acoustical guidance contact. As no other sounds were produced by the mother, it is obvious that the orientation signals of the mother acted as guidance signals for the young. My first experiments were done on *Vespertilionid* bats, but the same behaviour has been observed in horseshoe bats. KULZER (1961) published similar results for *Molossidae*. In this research it takes much time and effort to make slow progress.

Data concerning the communicative role of orientation signals in bats are still rather scanty, and it is necessary to direct more research effort towards studying the communicative character of these signals. The opinion that orientation signals have meaning only in the operation system of echolocation oversimplifies the problem and may prove dangerous. Facts important to the designing of animal sonar system models may be overlooked. Future experiments should try to answer two questions:

1. To what degree do animals use sounds having a primary communicative character to produce a kind of primitive sonaring?
2. To what degree do signals which are used for sonaring also act as communication signals?

It may not seem to be very profitable at the present time to speculate on the evolution of animal sonar systems, but in the future we shall certainly be brought face to face with the problem. In that case, it will be necessary to seek answers to the two above-mentioned questions.

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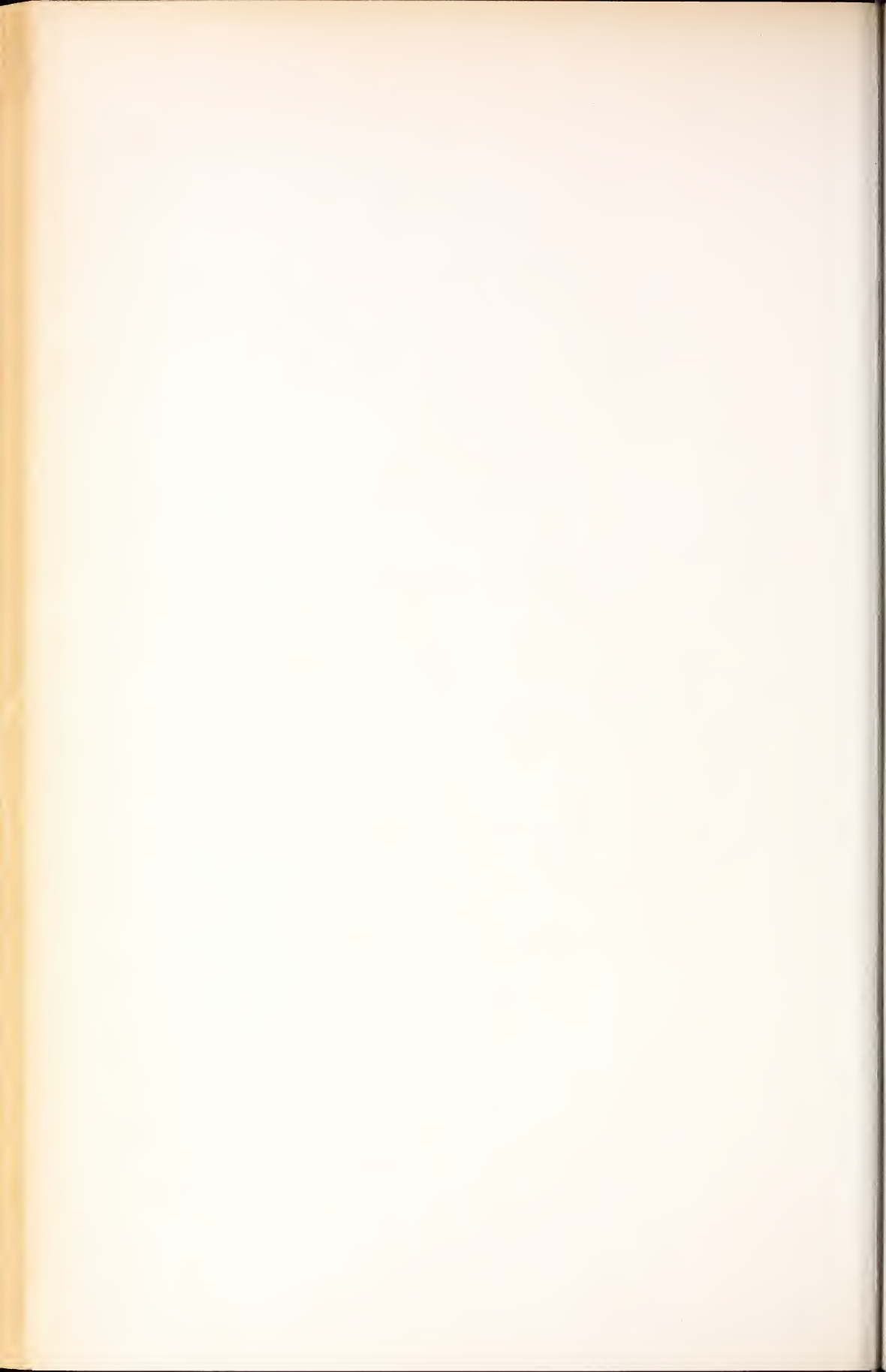
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VIII

Structures neurologiques impliquées
dans les systèmes sonars biologiques

Neural processing involded in sonar



THE PERCEPTION AND ANALYSIS
OF BIOSONAR SIGNALS BY BATS^{Ball} by
O. W. HENSON, Jr.

INTRODUCTION

The ability of bats to avoid obstacles without the aid of vision has been a subject of interest since the studies of Spallanzani in 1794 (11, 15). The idea of a sonar system involving the emission of ultrasonic pulses and the subsequent perception of echoes, was first suggested by Hartridge (28) and later verified by Griffin and Galambos (13, 16), Dijkgraaf (7), and others. Studies have revealed that the bat's sonar system not only permits the animals to avoid obstacles but also to localize, track and capture insects at rates of up to two per second, to select one insect from a swarm of many, and to capture prey resting on vegetation, solid objects and beneath the surface of water (15, 19, 25, 76). To account for these skills it must be assumed that bats can resolve closely spaced and even overlapping stimuli, and that they can extract a great deal of information from echoes.

If, however, consideration is given to the physical characteristics of bat sonar signals and known principles of physiological acoustics, several questions arise as to the ability of an auditory system to function efficiently under actual echolocative conditions (15). It is known, for instance, that the sensitivity of the mammalian ear for the second of two closely spaced stimuli is governed primarily by the intensity of the first stimulus and the duration of the interstimulus interval (37, 70); the louder a pulse and the shorter the echo delay,

the greater should be the loss in sensitivity for echoes. Another sensitivity reducing factor is the overlap of two sounds such that one partially or totally masks the other.

The commonly studied Vespertilionidae and Molossidae utilize pulse types characterized by brief durations (0.2-5 msec), average peak-to-peak sound pressures well above 100 dB (re-0.0002 dyne/cm²), and fundamental frequencies which sweep downward one octave or less over the duration of each pulse (15). The echoes of these FM cries normally return to the animal's ears within a few msec after the completion of each pulse and at a time when the ear should be relatively insensitive; Rhinolophidae (42, 46) and certain representatives of the neotropical genus Chilonycteris (17, 47) emit pulses characterized by long durations (7-100 msec) and high sound pressures. The fundamental frequency, however, is essentially a pure tone except for the terminal few milliseconds of each pulse where the frequency sweeps downward, in a manner similar to that of the FM type. The intense pure tone component of these pulses continues to be emitted while echoes return to the ear and a perfect echo-masking situation appears to be established.

To counter these problems it has been suggested that bats blank-out the emitted pulse, either by peripheral auditory mechanisms, such as the middle ear muscles (29), or by neural mechanisms of inhibition (20, 21, 73, 74). Other investigators have suggested that bats perceive beat-notes created by pulse-echo overlap (34, 35, 55, 56, 57), analyze time difference tones (45), or rely on pulse compressional mechanisms (71). When consideration is given to variations

in pulse types and the time relationships of sonar signals it becomes apparent that none of these theories can be applied satisfactorily to all species. How can the system efficiently perceive overlapping echoes if the system is suppressed during pulse emission? How can time difference tones be produced when there is no silent interval? How can beat-notes be produced if there is no overlap?

The following report is a review of the chiropteran auditory system and the physiological mechanism related to echo perception. By examining the capabilities of the system and its performance under artificial and actual echolocative conditions it will be shown that the bat's auditory system is extremely sensitive to FM echoes of self-emitted cries. It will be shown that common mechanisms can be applied to both 'pure tone' and FM bats and, that it is these mechanisms which permit the system to operate efficiently under what would otherwise appear to be adverse conditions.

THE AUDITORY SYSTEM OF BATS

Peripheral Processing

The peripheral processing of sonar signals involves the collection of sound waves by the external ear, the transfer of vibratory energy across the middle ear to the fluids of the cochlea and stimulation of sensory hair cells.

The external ear

The external ears of bats vary in size, shape and structure. In some species (Myotis, Glossophaga, Chiromeles) the ears are relatively small and simple; in others (Plecotus, Macrotus, Antrozous) the pinnae are large and their length may approach that of the animal's body. Extremely funnel-shaped ears, with the lower borders attached near the corners of the mouth, are found in Mormoops; in Eumops and other Molossidae the two pinnae may be fused across the midline. While the significance of these morphological variations is not clear, there is no doubt that the external ears can have an important influence on auditory sensitivity.

Studies on man (83) and cat (9) indicate that the external ear may increase the sound pressure at the tympanic membrane relative to that in the free-field. This funnelling effect is of little importance at frequencies below 1 kHz, but at higher frequencies the effect tends to become increasingly significant. In cats, for instance, removal of the pinnae does not hinder low frequency sound perception but may result in a 15-20 dB hearing loss for 16 kHz tones. Although there is some question as to whether the external ears of bats increase ultrasonic pressures at the tympanic membrane by more than 5-10 dB (26), it is clear that auditory sensitivity is highly dependent on ear orientation with respect to that of a sound source. By the selective blocking or enhancement of sound waves reaching the tympanic membrane, significant degrees of directionality are added to

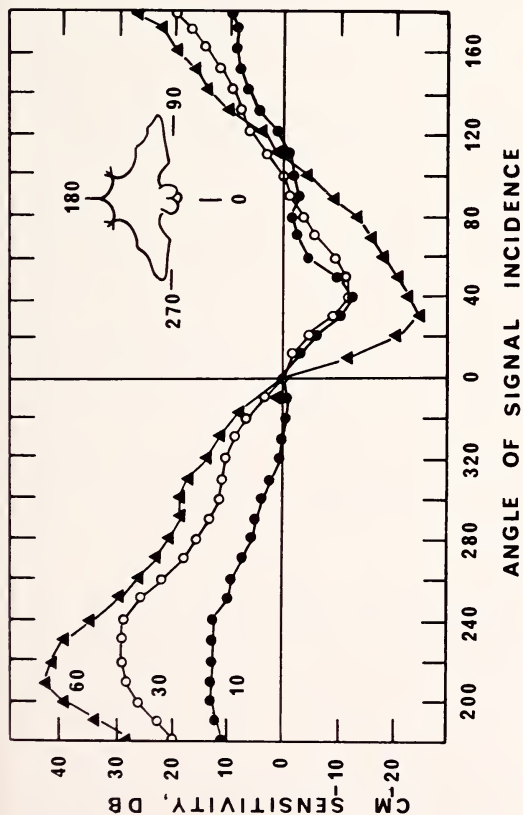


Fig. 1. Directional sensitivity of the left ear in *Tadarida* to 10 kHz, 30 kHz and 60 kHz tone pulses. Directionality is illustrated by showing the difference in cochlear microphonic sensitivity to sounds arriving from directly in front of the animal (0 degrees and 0 dB) as compared with those arriving from other angles in the horizontal plane.

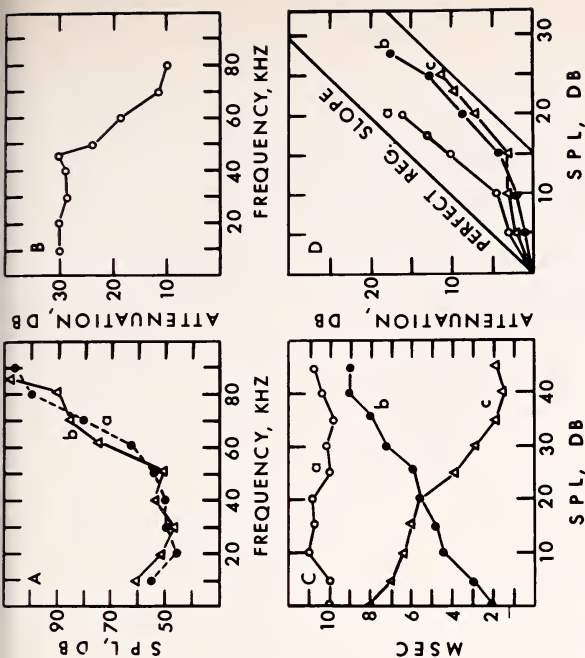


Fig. 2. The reflex characteristics of the middle ear muscles in *Tadarida*; A. the reflex threshold and 10uV cm audiogram; B. maximum attenuation of cochlear potentials produced by tympanic muscle contractions in response to high frequency sounds; C. reflex time relationships relative to stimulus intensity; and D. the relationship between stimulus intensity and the attenuation of cochlear potentials. The diagonal lines indicate the slope that would be attained if the increase in CM attenuation equalled the increase in the level of the stimulus. The above curves are based on studies carried out on unanesthetized bats with electrodes chronically implanted on the round window of the cochlea (31).

the system. This has been shown by determining cochlear microphonic (CM) sensitivity (31), evoked neural response sensitivity (20, 23, 26) and variations in auditory unit response patterns (72) with changes in the position of a sound source.

The CM directional sensitivity curves shown in Fig. 1 illustrate the greater degree of directional sensitivity for high frequencies than for low frequencies; also an angle of maximum sensitivity and the barrier effect of the head and body are evident. It is clear from these curves showing directional sensitivity in the horizontal plane that large differences in sound intensity may exist binaurally and, in the case of frequency modulated sounds, both intensity and frequency differences can occur at the two ears. No attempts have been made to determine CM directional sensitivity in the vertical plane or after removal of the pinnae. Neurophysiological studies on Myotis and Plecotus, have shown, however, that auditory units are sensitive to small changes (1-2 degrees) in the location of a sound source in both horizontal and vertical planes (23, 26). The role of the pinnae in providing directional characteristics is especially evident in the long-eared bat, Plecotus, where simply glueing the two ears together by their medial edges may produce a 10 dB gain in sensitivity in one ear while creating a 15 dB loss in sensitivity in the opposite ear (20).

The tragus, prominent in most species, also seems to influence the directional characteristics of the system. This structure,

located in front of the external auditory meatus, appears to sharpen directional sensitivity by partially blocking sounds from entering the meatus. Its removal increases, by 10 dB or more, the neural sensitivity to sounds (45 kHz or higher) below the horizontal plane and also results in a marked 30 degree broadening of the angle of maximum sensitivity (23, 26).

In addition to the tragus, many bats also have valve-like structures at the entrance of the meatus. When intense tones are presented to the ear, complete meatal closure may occur. Wever and Vernon (82) have suggested that this may provide some protection against acoustic trauma since pushing these valves together in anesthetized Myotis produced from 20-40 dB attenuation of cochlear potentials.

The pinnae of bats are well equipped with both intrinsic and extrinsic musculature (66, 67) and changes in the orientation of the pinnae undoubtedly alter directional sensitivity. In bats which emit short FM pulses the pinnae are thought to remain relatively fixed in position during flight and pulse emission. In Rhinolophus, however, pulse emission is accompanied by a forward movement of one ear and a backward movement of the other ear, even at fast pulse repetition rates (18, 58, 67). If deprived of the use of ear muscles, Rhinolophus nod their heads vigorously (67). In Chilonycteris, on the other hand, vigorous head movements appear more prominent than ear movements. Thus, species known to emit long pulses with relatively pure tone

characteristics appear to sample the sound field environment continuously or depend on mechanisms which seemingly modulate the acoustic input. The possible significance of these ear movements will be considered later in this report.

It is obvious from the above that the external ear can have considerable influence on the physical characteristics of sound waves reaching the tympanic membrane. Because of the dependence of directional sensitivity on frequency, it appears that much more information about the localization of a target and its physical characteristics may be gained by using FM rather than pure tone sonar signals.

The middle ear

The minute oscillations in atmospheric pressure (sound) that reach the end of the external auditory meatus cause the tympanic membrane to vibrate and the resulting vibratory energy is transferred from the tympanic membrane to the fluids of the inner ear via the ossicular chain.

The significance of these middle ear structures becomes apparent when consideration is given to the problem of transferring sound energy to the cochlear fluids. Acoustical properties of air and water are such that only 0.1% of the energy contained in an aerial wave will be transferred to a fluid body; the remaining 99.9% will be reflected. To solve the problem of efficient energy transfer an acoustic transformer is needed to match the resistances or impedances

of the two media (80).

There appear to be two major means by which the middle ear structures provide mechanical advantages for impedance matching. One, based on hydraulic principles, is offered by the ratio of the area of the tympanic membrane to that of the stapedial footplate. A second is provided by the ratio of ossicular lever arms (manubrium of malleus: long process of incus). Measurements of these ratios have been made in a number of different species of bats (30), and the total mechanical advantage offered by middle ear structures appears to be above 100 in most species. If the ear drum or ossicular chain is damaged there will be a mis-match of impedances, sound energy will be reflected rather than absorbed, and hearing impairments will result, as shown by Wever and Vernon (81) in their studies of cochlear potentials in Myotis.

Delicate middle and inner ear structures require protection from high sound pressures. The need for this protection has also been demonstrated in anesthetized bats (10, 81) and other mammals by recording cochlear potentials elicited by sounds of high intensity. As the intensity is raised from a threshold level the amplitude of cochlear potentials increases linearly in proportion to stimulus intensity. At high sound pressure levels the linearity is lost; the amplitude of the potentials falls, wave form distortion can occur and damage to the cochlear hair cells may ensue (70, 80).

These two muscles, especially the stapedius, are well developed

and richly innervated in bats (30, 82); their reflex activity is basically similar to that of other mammals except that the operating range is extended upward to include ultrasounds. Various curves showing the reflex characteristics of the middle ear muscles in the Mexican free-tailed bat (Tadarida brasiliensis mexicana) are shown in Fig. 2. These curves were determined from unanesthetized Tadarida with electrodes chronically implanted in the stapedius muscle or on the round window of the cochlea (31). There are four particularly important points revealed in these curves: (1) the reflex threshold is moderately low and has the same shape as the cochlear microphonic sensitivity curves (Fig. 2a); (2) the attenuation provided by muscle contractions is relatively constant over the 25-50 kHz range of frequencies included in Tadarida orientation cries (Fig. 2b); (3) the overall reflex time (latency plus contraction time) is consistently on the order of 10 msec regardless of stimulus intensity (Fig. 2c); and (4) the muscle contractions are delicately graded (Fig. 2d).

Prior to these studies on Tadarida it was suggested that the middle ear muscles might act as high-pass filters and assist bats in the perception of echoes in the presence of noise (30); this idea is similar to that recently advanced for man where the reflex does not affect, or may actually improve high frequency sensitivity (38). The bat's ear, however, is relatively insensitive to low frequencies and furthermore the tympanic muscle contractions provide a significant degree of attenuation over the frequency range of the emitted pulse.

Thus, the muscles do not function as high-pass filters as far as the 50-25 kHz sonar signals of Tadarida are concerned, although they may at higher frequencies.

The chief complaints of men with denervated stapedius muscles are that they hear too much and have difficulty understanding speech (38, 50). This and the fact that the threshold of the middle ear muscle reflex is moderately low and that contractions are delicately controlled has led a number of investigators to postulate that the muscles play an important analytical role in addition to their protective value. Simmons (68) has presented evidence that the tympanic muscles of cats increase the linear response range of the ear. It has also been suggested that their function is similar to that of the ocular muscles where rapid oscillations continuously change the input to the sensory cells (69). In another comparison, Lorente de No (39) has likened the middle ear muscle reflex to the pupillary reflex of the eye which continuously controls the amount of light stimulating the retina. In any event, there is good reason to believe that the middle ear muscles are important for sound analysis. Certainly they are capable of regulating the sound energy reaching the cochlea and in this way may limit the activity of the cochlear partition and the sensory nerve fibers.

The middle ear muscles are, however, ineffective in performing their functions when the total duration of the sound is short. In Tadarida the latency of the reflex is, at best, on the order of 1.5 msec and the time required for the muscle to attain a maximum

degree of contraction is approximately 10 msec. Thus, the middle ear muscle reflex is useless in dealing with brief bat pulses from an external source. In considering actual operational principles, however, it will be shown that middle ear muscle contractions prior to pulse emission provide a means of intensity control for hearing self-emitted sounds as well as echoes. Indeed, only by contracting in advance of pulse emission can protective and analytical functions be realized in echolocating bats.

The inner ear

While echoes reach the inner ear via external and middle ear channels, the emitted cries have an alternative pathway of transcranial bone conduction whereby laryngeal vibrations are transmitted directly to the cochlea. In many bats, however, the cochlea is loose in the skull; fat deposits occur between the larynx and cochlea; there is no firm union of the cochlea to adjacent skeletal elements; and the space between these elements and the cochlea is filled with blood sinuses, fat, or loose connective tissue. It has been suggested that these features isolate the cochlea acoustically and attenuate or prevent transcranial bone conduction of pulse energy (30). This could be advantageous when echoes overlap the outgoing cry as it might aid in preventing echo masking. In this respect it is interesting that cochlear isolation appears to be prominent in Chilonycteris, Rhinolophus and other species where pulse-echo overlap

normally occurs. No studies, however, have been carried out to determine the effectiveness of cochlear isolation for attenuating bone conduction at ultrasonic frequencies.

In addition to isolation from adjacent skeletal elements, the inner ear shows many features which suggest some degree of specialization for ultrasonic perception. The cochlea is relatively large and the basal turn, concerned with high frequencies, is particularly well developed. Within the basal turn the organ of Corti is small and the basilar membrane is narrow and tightly stretched. Special thickenings occur in relation to the basilar membrane and two osseous spiral laminae are present. In addition the round window is further along the basal turn than in most other mammals. These features are thought to raise the frequency range to which the organ will respond and increase its sensitivity to high frequencies (15, 57).

Inner ear responses to acoustic stimuli are of interest because this part of the system acts as a transducer for the conversion of vibratory energy into electrical energy and nerve impulses. One of the most useful techniques for studying cochlear activity is the recording of cochlear microphonic potentials. These are AC potentials with frequencies identical to those of the stimulus. While the origin of CM potentials is not known (79) they seem to constitute a link in the chain of events leading to sound perception. According to one theory the CM arises from polarizations of the cochlear hair cells and the cyclic AC characteristics are produced by the velocity of cellular deformations (80).

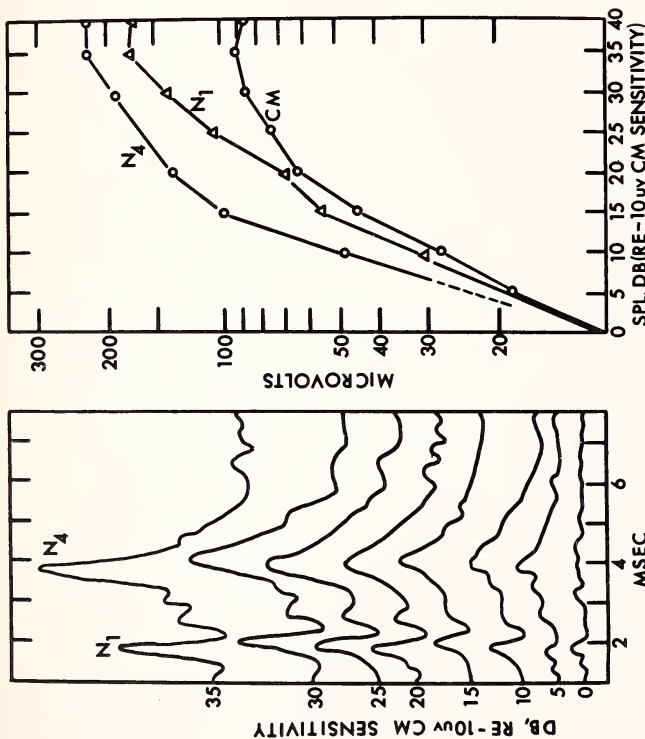


Fig 3. Intensity-function relations of auditory potentials in anesthetized *Chilonycteris parnellii*. A. The evoked neural potentials recorded with an electrode in the inferior colliculus; the positive neural response peaks (N_1 - N_4) and their growth in amplitude with increasing stimulus intensity are shown. B. typical input-output function of the cochlear microphonic potential (CM) recorded from the round window and N_1 and N_4 recorded from the inferior colliculus. Stimulus was 32 kHz, 1 msec pulse with 0.5 msec rise-decay time. Sound pressure levels are in dB relative to that required to produce a 10 uV CM potential.

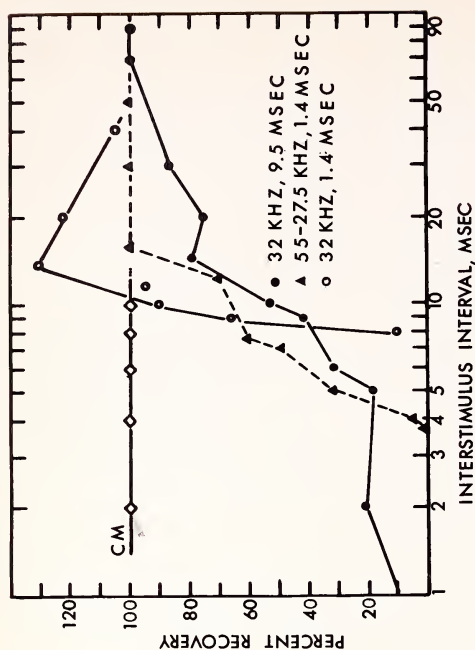


Fig. 4. Effect of inter-stimulus interval on the amplitude of the evoked N_1 response in *Chilonycteris*. The stimuli were short trains of 90 dB (re-0.0002 dyne/cm²), 0.5 msec rise-decay pulses. The 100% amplitude response was that evoked by single pulses delivered to the ear at a repetition rate of 1/sec. Note CM amplitude decreases markedly as the interstimulus interval falls below 15 msec.

Cochlear potentials have no real threshold or latency and, except at high sound intensities, their amplitude rises as a linear function (semi-log plot) of the sound pressure (see Fig. 3); thus, the CM potential can be used to assess cochlear sensitivity, the frequency of a stimulus and the amount of sound energy reaching the cochlea. By monitoring these potentials in active bats the exact time of pulse emission and echo return can be recorded.

Studies of the CM in Vespertilionidae (10, 81) and Tadarida (31) have revealed cochlear activity in response to sounds ranging from less than 1 kHz to more than 100 kHz. Evoked neural potentials have been recorded over the same range (20, 21, 72). These and recent behavioral studies (4) indicate that bats not only hear these sounds but that the peak sensitivity of the system for certain frequencies included in the orientation cries may be on the order of zero dB.

Central Processing

central nervous system

Many attempts have been made to establish the mechanisms involved in the neural processing and coding of sonic information. In no case, however, is there a complete understanding of any one part of the system. Many problems arise because of the complex nature of the component parts; these complexities are apparent even from brief descriptions limited to the classical auditory pathways (1, 53, 61).

In mammals the number of primary neurons in the spiral ganglion of the cochlea is approximately equal to the number of cochlear hair cells, but the dendritic processes of each neuron are associated with two or three internal hair cells and many external hair cells. The central connections of first order neurons are with the ventral and dorsal cochlear nuclei primarily, but many axons also send branches to the contralateral olivary complex.

The main projections arising from the cochlear nuclei travel in three stria (dorsal, intermediate, and ventral) which converge near the contralateral superior olivary nucleus where many fibers terminate. As they cross the brain stem, some fibers also terminate in the ipsilateral superior olivary nucleus while others synapse with neurons scattered about the ventral stria or trapezoid body. Some fibers arising from the cochlear nuclei ascend in the lateral lemniscus with third order fibers arising from the olivary complex. These fibers, as well as those arising from cells within the lateral lemniscus pass primarily to the inferior colliculus but some join efferent fibers from the colliculus and pass to the medial geniculate body via the brachium of the inferior colliculus. From the medial geniculate body fibers pass to the auditory cortex in the temporal lobe.

The entire system is much more complicated than this brief description indicates. In the cochlear nucleus, for instance, a single cochlear nerve fiber may contact 13 distinct regions and establish synaptic connections with hundreds and perhaps thousands

of neurons which may themselves be of many different types. Indeed, the entire cochlea may be projected many times to a given nuclear complex; furthermore, the neurons may feed back to themselves or back to the same nuclear areas from which they originated. In addition to the classical auditory pathways described above, diffuse reticular pathways exist. Furthermore, the ascending system is more or less paralleled by a descending system extending from the cortex to the cochlear hair cells. (60, 61).

The ascending auditory pathways and nuclei of bats are unusually large (20, 40, 84). In some bats they reach a larger size, relative to brain size, than is known in any other mammal. The enlarged portions of the system are, however, limited to the mesencephalic centers (cochlear nuclei, trapezoid body, olivary complex, inferior colliculi). Higher centers, the medial geniculate body and auditory cortex, are not so remarkable in their development. The temporal lobe (auditory cortex) of bats is said to be one of the most primitive among mammals, not even showing the typical six layered structure (63). The greater development of the lower centers has led to the conclusion that the auditory system of bats operates predominately at the mesencephalic level and that its main function is the relay of auditory impulses to motor centers (53). Studies on cats, however, have shown that the auditory cortex is not essential for determining threshold sensitivity or for the discrimination of frequency (3, 44, 62, 77) or intensity (59, 64),

but it does seem to be important for sound localization (41, 43) and for the discrimination of changes in the pattern of presentation of two tones (6). The poor development of the temporal cortex in bats seems to correlate with views of its relatively minor role in auditory analysis. Although there is some evidence that neural processing can occur between the inferior colliculi and temporal cortex in Myotis (75) Konstantinov (36) has shown that the application of γ -aminobutyric acid to the temporal cortex (resulting in functional exclusion) does not impair the ability of bats to detect and avoid wire obstacles. The fact that localization is not impaired after exclusion of the auditory cortex is one line of evidence in agreement with Grinnell's (23) view that binaural intensity differences, rather than time differences, are the main localization cues for bats.

The spread of neural impulses to the auditory centers has been studied with the aid of both gross and microelectrodes. Responses recorded from anesthetized bats indicate that information is rapidly dispersed throughout the system. Auditory nerve potentials (N_1) are generally recorded within 0.8 msec after the presentation of a stimulus and roughly 0.5-1 msec is required for impulses to reach each of the higher centers. What appear to be second (N_2) and third (N_3) order response peaks in Myotis occur with latencies of 1.5 and 1.9 respectively and collicular input (N_4) responses usually reach a peak within 2.8-3.0 msec after stimulation of the ear. Electrodes placed in the medial geniculate body detect activity

in about 5 msec and cortical evoked responses begin to appear within 11-15 msec (20,21).

Perhaps more important than the rapidity of the spread of information are the neurophysiological data obtained from single auditory units which indicate the multitude of neural components and the capabilities of the system to perceive and code specific information. Microelectrode studies by Grinnell (20, 21) and Suga (72, 73, 74, 75) have shown that 'onset' units are the characteristic type throughout the bat's auditory system. Each neuron of this type has a best frequency, defined as that frequency where the intensity of the stimulus required to fire the unit is lower than that which will excite it at any other frequency. The response areas for many auditory units have been determined by finding the best frequency and all other frequencies to which a neuron will respond.

The variations in shape of unit response areas in bats are similar to those described in other mammals; on the basis of shape, response areas may be classified in one or several categories such as symmetrical or asymmetrical, narrow or broad, and closed or open; they may further show more than one frequency peak, sometimes separated by an insensitive area. Stimuli falling within certain parts of the response area of cochlear nuclear units may evoke after-discharges which change the response characteristics of the unit to subsequent stimuli. If unit excitability, after-discharges, or spontaneous activity decreases or ceases in response to a subsequent stimulus the unit is inhibited; if the firing rate or excitability increases, it is facilitated. The response areas of neurons may contain or may be bounded or separated by inhibitory or facilitatory areas such that their response to a given stimulus may be influenced by previous activity and their existing state.

In addition to onset units, other neurons are known to discharge impulses spontaneously at various regular or irregular rates and also show complicated patterns of inhibition and facilitation depending on the nature of the stimulus and previous neural activity. Each neuron also has a specific refractory period of 0.3-0.5 msec during which it cannot be re-excited.

The existence of descending auditory pathways and the numerous provisions for feedback control in the CNS are particularly interesting in view of recent studies which have outlined their possible roles in sound analysis. Efferent and centrifugal fibers may have a considerable effect on the firing pattern, best frequency, response area and latency of single units (8), and they appear to play a role in focusing and defocusing the sensitivity of the system on a certain band of frequencies (51, 52). The phasic response characteristics, the extremely narrow response areas of some inferior collicular units, and the closed tuning curves described in Myotis by Grinnell and Suga seem to be determined by inhibitory and excitatory interaction within the system.

In general, the physiological characteristics of auditory units in bats do not differ from those described in other mammals. In contrast to cats and monkeys, however, bats appear to have fewer cochlear nuclear units with spontaneous activity, but many (not described in other mammals) which show after-discharges following excitation. The inferior colliculus of bats, in comparison with other mammals, appears to have more units characterized by phasic 'on' responses and more with closed response areas; the latter are excited primarily by sounds of relatively low intensity (21, 72, 73, 74, 75).

The significance of units with different best frequencies, response areas, after-discharges and inhibitory areas is unclear for it is not known how specific auditory information is synthesized. It seems likely, however, that frequency analysis is, at least in part, determined by the association of specific nerve fibers with specific areas of the cochlear partition since the mechanical activity of the basilar membrane varies as a function of frequency (2). Frequency specific fibers tend to be tonotopically arranged (20, 21) and with a given frequency the information may be conveyed over certain assigned channels to specific parts of the auditory nuclei (5). The channelling of information to units with narrow response areas could be important in fine frequency analysis; variations in unit discharge patterns could also play a role. On the basis of narrow response areas of inferior collicular units in Myotis, Grinnell (21) has suggested that bats can make fine frequency discriminations, perhaps to within a few hundred cycles. Many units respond differently to changes in intensity as well as frequency and it appears that both intensity and frequency information may be coded by most auditory units. The best neural correlates of intensity coding are changes in latency, firing rate and the total number of units responding. Grinnell found many inferior collicular units where the intensity changed the unit response latency by as much as 4-5 msec. The latency change with intensity also appears to be reflected in the latency of the middle ear muscle reflex (fig. 2c). Intensity coding by unit discharge rate is limited in the auditory system. Inferior collicular units in Myotis have been observed to change their firing rate with changes in intensity but

only over limited ranges (21, 72); most auditory units increase their firing rate over intensity changes of 20-25 dB or less (12, 33). The best neural correlate of intensity coding is the number of units responding; the summed neural responses (N_1 - N_4) increase in amplitude as the stimulus intensity is raised (see Fig. 3). On the basis of responses recorded from Myotis it has been estimated that intensity differences of less than 1 dB (0.5 - 0.2) may be discernible (21). Because of the highly directional characteristics of the bat's ears to ultrasounds and the apparent ability of the system to assess small intensity differences, an accurate neural basis for target localization is provided. Binaural time delays and phase differences that seem important for the lateralization of sound in man, at least at low frequencies, have not been shown to be involved in bat sonar and in theory would not appear to apply (23, 26).

Only 3-5 cycles of an ultrasonic pulse are needed to excite the phasic onset units of the bat's auditory system and since neural (N_4) audiograms are not altered by variations in stimulus duration, it appears that precise frequency analysis can be accomplished with only brief (0.2 - 0.3 msec) exposure of the ear to a stimulus (21). Although most units appear to respond only to the onset of a stimulus others respond continuously over the duration of a sound; in the latter the threshold may change drastically with stimulus duration. In one Myotis unit Grinnell found a 40 dB change in threshold as the stimulus duration changed between 1 and 1.75 msec. Units have also been described which are reversibly inhibited by increases in stimulus durations and a few units exist which show both 'on' and 'off' responses to a pure tone stimulus. Cochlear

nuclear units with after-discharges could be involved in duration analysis as well as interstimulus interval measurements since the duration of the after-discharges varies with stimulus duration (the longer the duration, the longer the after-discharges continue); the after-discharges, however, may be inhibited by a subsequent stimulus (72). Some units show short term facilitation, and distinct responses to stimuli separated by 0.3-0.5 msec occur; other units appear to respond only to a second stimulus under certain conditions (22).

For the most part physiological studies on the auditory system of bats have been restricted to the cochlea, the cochlear nucleus, and inferior colliculus. These studies have shown that hearing in a given species is most sensitive to frequencies included in the orientation cries. Neurophysiological evidence of fine discriminations of frequency, intensity, sound duration, sound localization, and silent intervals has also been presented. Indications that all the physical characteristics of sonar signals can be perceived and analyzed argue against beat-note and time difference tone theories. As noted previously, these theories were offered in part as a solution to the problem of perceiving faint echoes after the emission of a loud pulse or the operation of the system in the presence of pulse-echo overlap. While some units can respond to stimuli separated by as little as 0.3 - 0.5 msec, the majority of units, especially in the inferior colliculus of bats seem unable to respond to a test stimulus closely following a loud preconditioning stimulus. It might be argued that the rapid recovery of only a few units is all that is necessary for echo perception; on the other hand, by comparing neural responses in anesthetized

bats with responses recorded from echo-locating bats, it will be shown that there is a marked improvement in the performance of the system in the echolocating animal over that observed in anesthetized ones.

PHYSIOLOGICAL CORRELATES OF PULSE-ECHO

PERCEPTION IN ANESTHETIZED BATS

If single pulses are delivered to the ear of an anesthetized bat and evoked potentials are recorded with gross electrodes implanted in the inferior colliculus, the neural response shows four positive peaks followed by a negative slow wave. As discussed by Grinnell (20, 21) the positive peaks (designated N_1 , N_2 , N_3 , and N_4 in reference to their time of appearance) probably represent the activity of 1st, 2nd, 3rd, and 4th order neurons respectively; the slow wave appears to be the summed response of many postsynaptic (inferior collicular) units. This is suggested by the fact that the slow wave occurs during the time of inferior collicular unit activity. Also, the slow wave may be abolished by the application of synaptic inhibitors or by the destruction of postsynaptic cells whereas the positive peak is not affected (14, 54).

As shown in Fig. 3, the amplitude of the evoked response is dependent on stimulus intensity; as the intensity is raised from a threshold level the amplitude steadily increases as more and more units are excited. In Chilonycteris a maximum response amplitude was reached when the stimulus intensity was 35-40 dB above the intensity which evoked the smallest detectable response. With further increases in intensity the response amplitude usually remained stable or decreased slightly. The reasons for stabilization or reduction in amplitude at high intensities is not entirely clear, but the CM amplitude may fall or stabilize at high

intensities and there is a limit to the total number of fibers capable of responding. Also as noted above many collicular units in Myotis have closed response areas, i.e., high intensity as well as low intensity thresholds; these would not be expected to respond to intense sounds (21).

By maintaining stimulus sound pressures below those which overdrive the system and by simultaneously recording CM and N_4 potentials, it is possible to monitor changes in the sensitivity of the system to pairs or trains of stimuli. Also in this way it is possible to determine the ability of the neural portion of the system to follow accurately the information presented to it by the cochlea. Fig. 4 shows the result of one such experiment on anesthetized Chilonycteris (37°C). Short trains of 90 dB, FM and pure tone pulses (with frequencies similar to those included in the emitted pulses) were delivered to the ear and the effect of interstimulus intervals on the amplitude of evoked potentials was recorded. In this and similar experiments on Tadarida molossa and Molossus milleri (unpublished), the CM amplitude remained stable regardless of the pulse repetition rate or interstimulus interval; the neural potentials, however, showed a decrease in amplitude as the interstimulus interval decreased.

A reduction of approximately 40% occurred in the amplitude of evoked responses when stimuli were separated by 10 msec and a reduction of 80% or more occurred when the interval fell below 5 msec. In the same bat the attenuation of stimulus intensity that was required to reduce the amplitude of the evoked response from its 100% value at 90 dB to its 20% value was 35 dB; thus, with a 5 msec interstimulus interval the loss in sensitivity appears to be on this order of magnitude. When pairs of

identical 90 dB pure tone or FM pulses were used the same effect was observed. To date, only limited observations have been made on the effect of intensity on recovery cycles in Chilonycteris; with more intense stimulus sound pressures the recovery times were longer while with fainter stimuli the recovery times were shorter than that shown in Fig 4. In this respect, Grinnell's studies (22) of recovery curves in Myotis are of interest for they show that sensitivity for the second of two identical sounds separated by 2 msec improves about 10% for every 10 dB of stimulus attenuation. For intensities within 30 dB of threshold, however, it appears that there may be an actual increase in sensitivity for the second stimulus; some units which do not respond to a first stimulus appear to be facilitated, respond to the second stimulus, and elicit a supranormal N_4 response. Because N_1 was observed to recover more slowly than N_4 , Grinnell has suggested that special facilitatory mechanisms exist between the cochlear nuclei and inferior colliculi. Although fast recovery has been described with faint stimuli, Grinnell found that almost half of the inferior collicular units isolated in Myotis has recovery periods of at least 10 msec. The explanation for this, as well as the reduction of the N_4 observed in Chilonycteris, seems to lie in the finding that following excitation, most auditory units in the inferior colliculus are typically inhibited and the period of inhibition is dependent on stimulus intensity. In 21 of 23 inferior collicular units studied by Suga (73), inhibitory periods after excitation ranged from a few msec to more than 100 msec. In the commonest type of unit in Myotis the period of inhibition was 10-17 msec; only a few collicular units had no inhibitory period. Since

the inferior colliculi are extremely well developed in bats, and seem to be essential for auditory analysis, it is somewhat surprising to find that the majority of units have relatively long recovery or inhibitory periods after excitation. If this inhibition existed under actual echolocative conditions the sensitivity for echoes would seem to decrease progressively as the pulse-echo interval fell below 15 msec; it would appear that the analysis of targets at distances of less than 2.6 m would become increasingly difficult as the distance decreased. From behavioral observations on bats, however, it seems that 1-2 meters is a maximum echolocative range for the detection of insects or fine wires (15, 25). Suga (73) has suggested that the inhibition may be utilized in time-delay or target distance analysis. Units with short inhibitory periods could respond to echoes returning from close targets while, with time, more and more units would recover and the number of recovered units might be indicative of target distance. The average recovery time seems much too long to account for an efficient performance of the system.

In Chilonycteris pulse-echo overlap occurs and no true silent period exists. Masking has not been studied extensively in Chilonycteris but preliminary studies have revealed its existence. If, for example, pure tone or FM pulses are delivered to the ear at relatively slow rates and a second loudspeaker delivers a masking stimulus consisting of long, pure tone pulses with long rise-decay times, the characteristic result in the bat is the same as that observed in other mammals; the amplitude of the evoked response to the test stimulus decreases as the intensity of the masking stimulus increases; the neural response may disappear

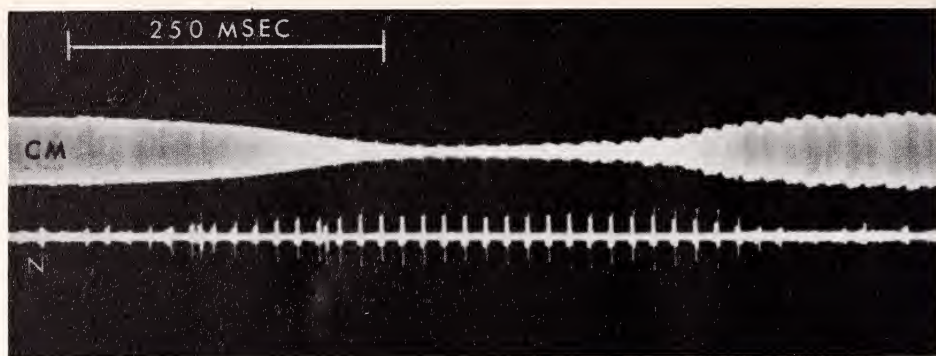


Fig. 5. Demonstration of masking in Chilonycteris upper trace shows CM potentials evoked by 32 kc pulse with long (250 msec) rise-decay time and the CM responses to 1 msec, FM (40-20 kHz) pulses delivered by a second loudspeaker. Bottom trace shows the evoked N_1 response recorded with a round window electrode; as the 32 kHz masking stimulus increases in intensity the evoked neural response decreases.

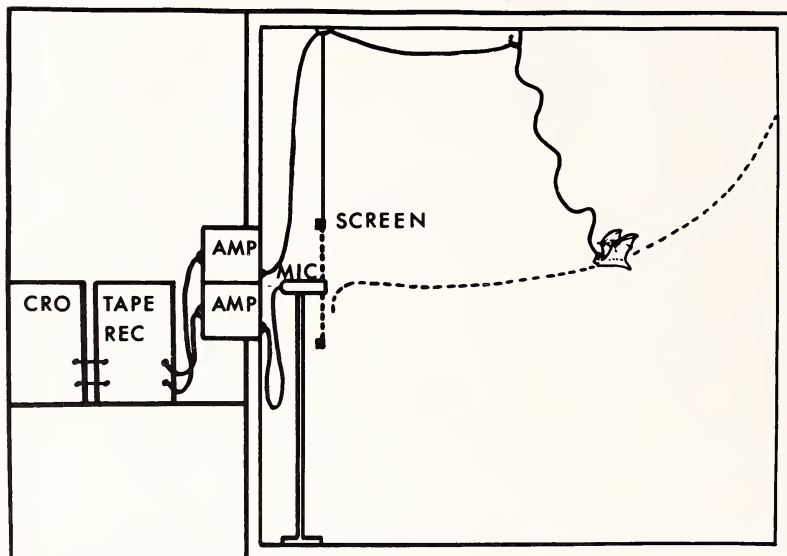


Fig. 6. Experimental set-up for recording potentials from flying Chilonycteris and Tadarida. The animals were released from one wall and flew across the room to land on the window screen. A microphone (MIC) placed behind and in contact with the screen recorded the emitted pulses and the time of landing. The walls of the chamber were completely lined with orlon pile to reduce reverberating echoes.

altogether if the intensity (signal to noise ratio) is high enough (Fig. 5).

Several factors may explain masking (24); the masking stimulus may lead to inhibition of units, or cause them to fire so that recovery has not occurred before the arrival of the test stimulus. If the masking noise is continuous, adaptation may occur, and in unanesthetized animals, contractions of the middle ear muscles might further decrease sensitivity to a test stimulus. In many respects the neural mechanisms of masking and the reduced sensitivity to the second of two closely spaced stimuli seem to be similar. The existence of many sharply tuned collicular units (gaining or losing sensitivity at rates up to 35 dB/kHz) may be important for reducing masking since only very narrow bands of frequencies would be effective in masking these units (24). Such units, however, would seem to be of little value for Chilonycteris or Rhinolophus unless ear movements, flight speed or target movements created Doppler shifts in the returning echoes.

The best method for reducing masking is the orientation of one ear toward the signal of interest and the other toward the masking signal; in this way, interneuronal interaction reduces the masking effect of noise by as much as 20 dB (24). The synchronous ear movements which occur in Rhinolophidae could function in this manner. A forward moving ear would be expected to become more sensitive to the emitted pulse and a backward moving ear less sensitive. Thus, the signal (echo) to noise (pulse) ratio would change continuously

according to the orientation of the pinnae. Head movements, on the other hand, would have little effect in changing the pulse pressures reaching the ear, but at some instant the signal to noise ratio would be better than at any other time. If the purpose of these movements is to reduce the masking effect of the outgoing cry, the question arises as to why these bats don't use an FM pulse rather than a long pure tone terminated by an FM sweep.

If the FM sweep is the important part of the sonar signal then the mechanisms capable of improving the sensitivity of the system to closely spaced stimuli could be applied to all bats; the most important of these mechanisms would be one which reduced the pulse energy reaching the ear or reduced neural sensitivity during pulse emission. Important questions relevant to the understanding of these mechanisms are: (1) to what extent does the energy of the emitted pulse actually reach the ear; (2) do sensitivity changes occur during pulse emission; (3) to what extent are neural units excited by the emitted pulses and echoes; and (4) what is the relative importance of the pure tone and FM components in Chilonycteris sonar signals? Recordings of physiological potentials from active bats have provided some answers to these questions.

PHYSIOLOGICAL CORRELATES OF PULSE-ECHO PERCEPTION

IN ACTIVE BATS

Recording physiological potentials from active bats presents many problems. The necessity for long leads, line interference, movement artifacts, and neural noise are major obstacles. When recording CM

potentials these problems can be eliminated by the insertion of high-pass filter networks in the recording system (29, 30); in the case of neural potentials, however, the interference band covers that of the evoked responses. One method which has proved successful in eliminating these problems is the utilization of differential amplification in order to cancel noise and artifacts common to two electrodes. In three of five Chilonycteris parnellii good records were obtained when one recording electrode and the ground electrode were implanted in the midline, close together and just anterior to the inferior colliculi. With a second recording electrode placed in the inferior colliculus typical N_4 potentials were recorded differentially in response to acoustic stimuli.

By crimping miniature connector pin socket contacts (Amphenol, series 221) to the electrodes (uninsulated stainless steel insect pins, No. 00) the preparations could be connected or disconnected from the recording equipment. A 3 m length of 4 conductor, shielded cable (Alpha Wire Corp., No. 1107) was used to connect the animals to the recording equipment (Tektronix, series 122 pre-amplifiers and Precision Instrument Co. tape recorder, Model PI 6100). With a portion of the cable suspended from the ceiling of the recording chamber the animals usually flew well and did not seem to be hindered seriously by wires attached to and suspended above their heads. One Chilonycteris routinely flew in circles around the room and readily performed landing maneuvers. Two others were less willing to fly, but if coaxed to do so they performed reasonably well. Recordings

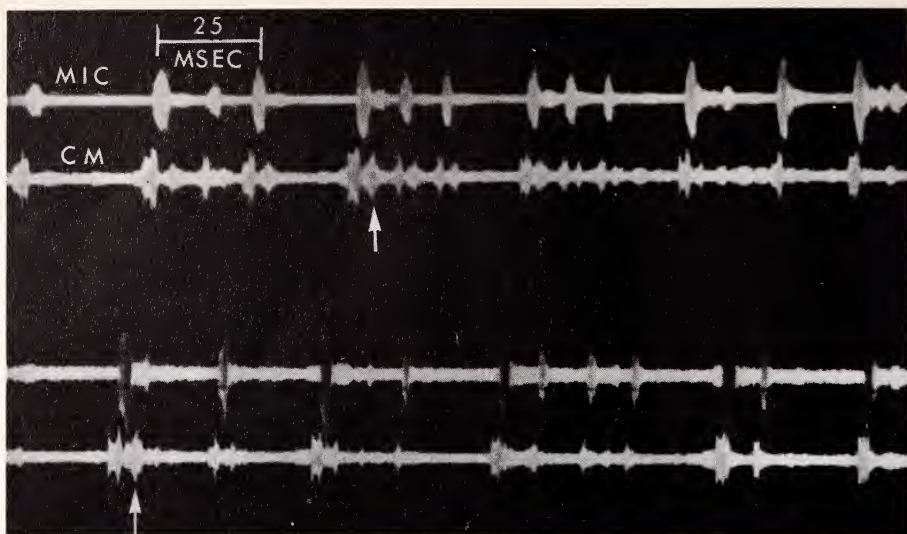


Fig. 7. Portions of two records showing pulse and echo-evoked CM potentials recorded from flying Tadarida. Upper trace shows the emitted pulse detected by the microphone. Lower trace shows CM potentials evoked by emitted pulses and echoes. Arrows point to high amplitude echo-evoked potentials.

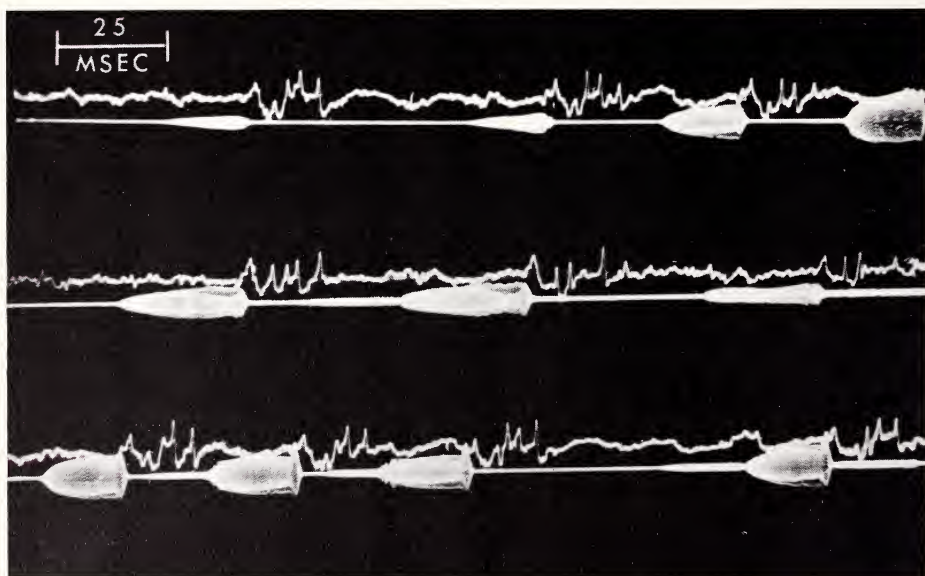


Fig. 8. Collicular (N_4) potentials recorded from Chilonycteris placed on the ceiling of the recording chamber (upper trace) and the emitted pulse as detected by a microphone (lower trace). Note relatively small amplitudes of responses evoked by the beginning of emitted pulses and the relatively large potentials evoked by the terminal FM sweep of both pulses and echoes.

were made from flying bats only after they appeared to be fully recovered as demonstrated by their ability to fly well and avoid obstacles. Most records were made 3-7 days post-operative. The results obtained from all three were consistent.

The recording chamber (approximately 3 m x 3 m x 3 m), illustrated in Fig. 6, was lined with orlon pile to reduce reverberating echoes. A framed, wire window screen (approximately 1 m x 1 m) suspended from the ceiling, served as a landing area and major echo source and a microphone placed behind and in contact with the screen recorded the emitted pulses and time of landing. The position of a bat in relation to the landing area was estimated by the delay between the time of appearance of pulse and echo-evoked responses or by the time delay between the pulse-evoked response and the arrival of the pulse at the landing area.

Records of CM potentials from one flying Tadarida are shown in Fig. 7. Here the pulse and echo-evoked potentials are readily distinguishable. Equal amplitude pulse and echo-evoked CM potentials were usually recorded when the bat was flying from one end of the recording chamber to the other end and when the echo delay was on the order of 5-6 msec. With echo delays of less than 5 msec the echo-evoked CM potential characteristically became smaller than the pulse elicited response even though the echo strength should have increased as the distance decreased. At short distances, when the pulses and echoes overlapped, the echo-evoked CM response often was higher in amplitude than the pulse-evoked response.

Echoes returning from a large target 1 m from the animal should have been considerably less intense than the emitted pulse. Assuming that the pulse energy falls off inversely as the square of the distance, the pulse SPL reaching the target should have been about 18 dB less than that 10 cm in front of the bat's mouth (15). Atmospheric attenuation over the 2 m round trip distance should have reduced the 30 kHz echo strength about 2 dB and the echo should have fallen at least 5 dB once reflected from the target and during its return to the animal's ears. Thus, 10 cm in front of the bat's mouth the pulse should have been at least 25 dB louder than the echo, but judging from the CM potentials, the pulse and echo energy reaching the cochlea were on the same order of magnitude. As noted above, the suppression of pulse energy reaching the ear should improve the neural sensitivity of the system to echoes. The studies of neural excitation by outgoing cries and echoes in Chilonycteris clearly show that this is the case; this is especially evident in the records shown in Fig. 8 where the bat was positioned on the ceiling of the recording chamber so that echoes from the walls and floor did not return to the animal until 3-15 msec after the beginning of the emitted pulse. Under these conditions little or no sign of neural activity was associated with the beginning of an emitted pulse; distinct positive N_4 peaks were seldom seen, but negative slow waves of relatively small amplitude occurred in about 75 percent of several hundred records examined. On the other hand, positive N_4 peaks and negative slow waves were consistently evoked by the terminal FM sweep of each pulse and by the FM sweep in returning echoes. Indistinct responses or no responses occurred at times when the pure tone

of the echoes should have overlapped the outgoing cry.

Most of the pulses emitted by Chilonycteris had relatively long rise times and it was first thought that this plus the pure tone itself, which would be expected to excite fewer units than an FM signal, might account for the small responses evoked by the beginning of the cries. When long rise-time pulses emitted by another Chilonycteris were presented to the animal's ears, however, the evoked responses often had prominent N_{II} peaks and/or prominent slow waves. Also when the animals were placed in small cages or in confined spaces the responses to the beginning of each pulse appeared to be more marked than when the animals were situated more than 50 cm from a wall or obstacle. Thus, overlap responses seemed to be evoked if the overlap occurred before the initial response to the beginning of the pulse was determined.

The fact that the FM sweep in the cry and returning echoes always evoked distinct responses implies that the FM sweep is an most important part of the pulse. The echo-evoked potentials are particularly interesting for they were often more prominent than pulse-evoked potentials; they were equal or higher in amplitude than pulse-evoked potentials even when the echo delay (inter-response interval) was as much as 15 msec, indicating an echo source distance of 2.6 m, the maximum echo delay under the recording conditions. In many cases high amplitude echo-evoked potentials occurred with as little as two msec between the N_{II} peaks and what appeared to be maximum amplitude N_{II} responses were evoked by the successive bursts of sound, separated by 5 msec, which occurred in loud audible Chilonycteris screeches. These finds indicate that the system is considerably more

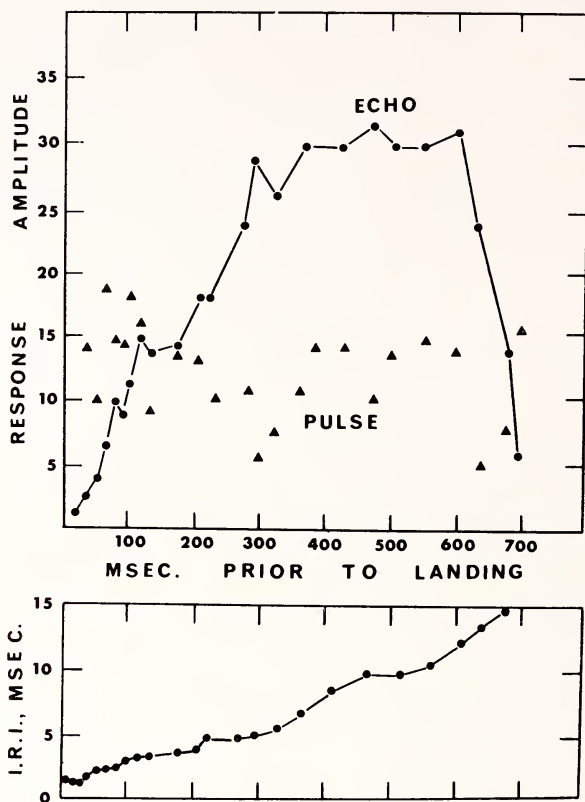


Fig. 9. Graph of amplitudes of pulse and echo-evoked N_4 potentials recorded during a typical landing (A), and curve showing the decreasing interval between pulse and echo evoked potentials as the animal approached the landing area (B). Note steady decrease in echo-evoked amplitude as the inter-response interval falls below 5 msec.

sensitive under actual echolocative conditions than under artificial conditions. There were, however, indications of reduced sensitivity immediately following pulse emission. When Chilonycteris were performing landing maneuvers, under the conditions shown in Fig. 6, there was always a steady decrease in the amplitude of the echo-evoked potentials once the pulse and echo-evoked response interval fell below 5 msec (Fig. 9). How much of this reduction was the result of the bat's turning in preparation for landing could not be determined; in spite of the reduction, echo-evoked responses were clearly evident even up to the moment the bats contacted the landing area.

Records of one landing are shown in Fig. 10 to illustrate the manner in which echo responses were identified. An indistinct positive peak and/or negative slow wave was associated with the terminal FM sweep of each pulse and following this an echo-evoked positive N_{LL} peak occurred; with time these two response peaks moved closer together, indicating the progressive decrease in echo delay as the animals approached the target.

Fig. 11 shows the emitted pulses detected by the microphone behind the landing platform and the neural responses recorded from the two inferior colliculi during different phases of echolocation in a typical landing. Marked echo sensitivity and directional sensitivity are apparent in these records. During the search phase (pulses 1-10), characterized by relatively long interpulse intervals, two distinct echo-evoked responses appear in the right collicular records as the bat became aligned with the target (pulses 6-10); the left collicular record generally shows only one distinct echo-evoked response. During the

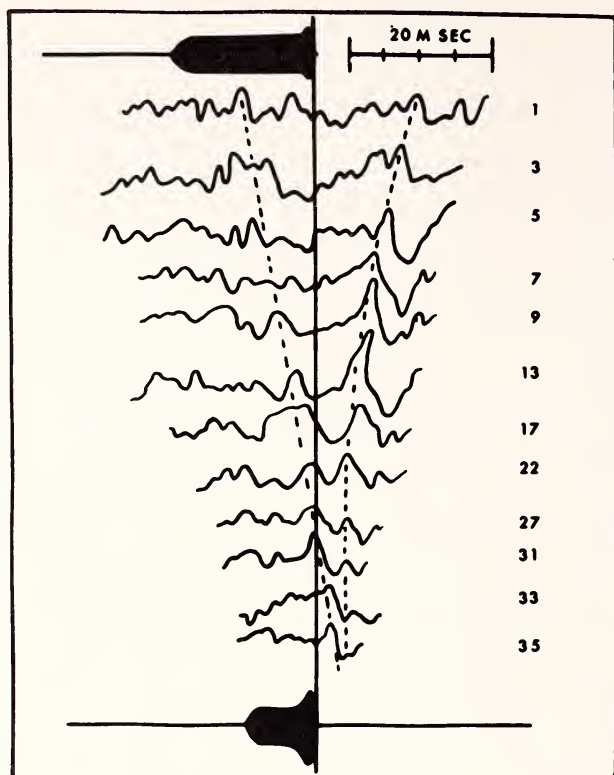


Fig. 10. Pulse and echo potentials evoked by the terminal FM sweep in flying Chilonycteris. The vertical line in the center represents the end of each pulse as detected by the microphone behind the landing area; the numbers in the right hand column represent the pulse number in the pulse emission sequence. Pulse 35 was the last pulse emitted before landing. The FM pulse-evoked responses associated with pulses 1-31 appear to occur before the end of each pulse because of acoustic delay. Converging dashed lines interconnect pulse and echo-evoked potentials.

approach phase (pulses 11-30), when the interpulse interval decreased and the bat was better aligned with the target, the potentials recorded bilaterally were somewhat similar (especially pulses 10-22); in addition, only one echo-evoked response occupies the interval between pulses. The FM component from the more distant objects should have returned during the time that the following pulse was being emitted. The absence of responses at this time suggests that echoes from the distant objects have been masked by the outgoing cry. Responses recorded during the terminal phase (pulses 30-43), characterized by short (1.5-4 msec) interpulse intervals, are difficult to interpret as the neural activity is very cyclic. The potentials recorded from the right colliculus, however, do show distinct echo responses even after the bat apparently turned in preparation for landing; what appear to be pulse-evoked responses during the terminal phase are probably the summed responses elicited by overlapping pulses and echoes.

The results obtained from active Tadarida and Chilonycteris indicate that the bat's sonar system is remarkably sensitive to echoes. The most plausible explanations accounting for the marked sensitivity to echoes are suppression of the system during pulse emission and facilitation immediately after. In the final part of this report the mechanisms which produce suppression and facilitation will be examined.

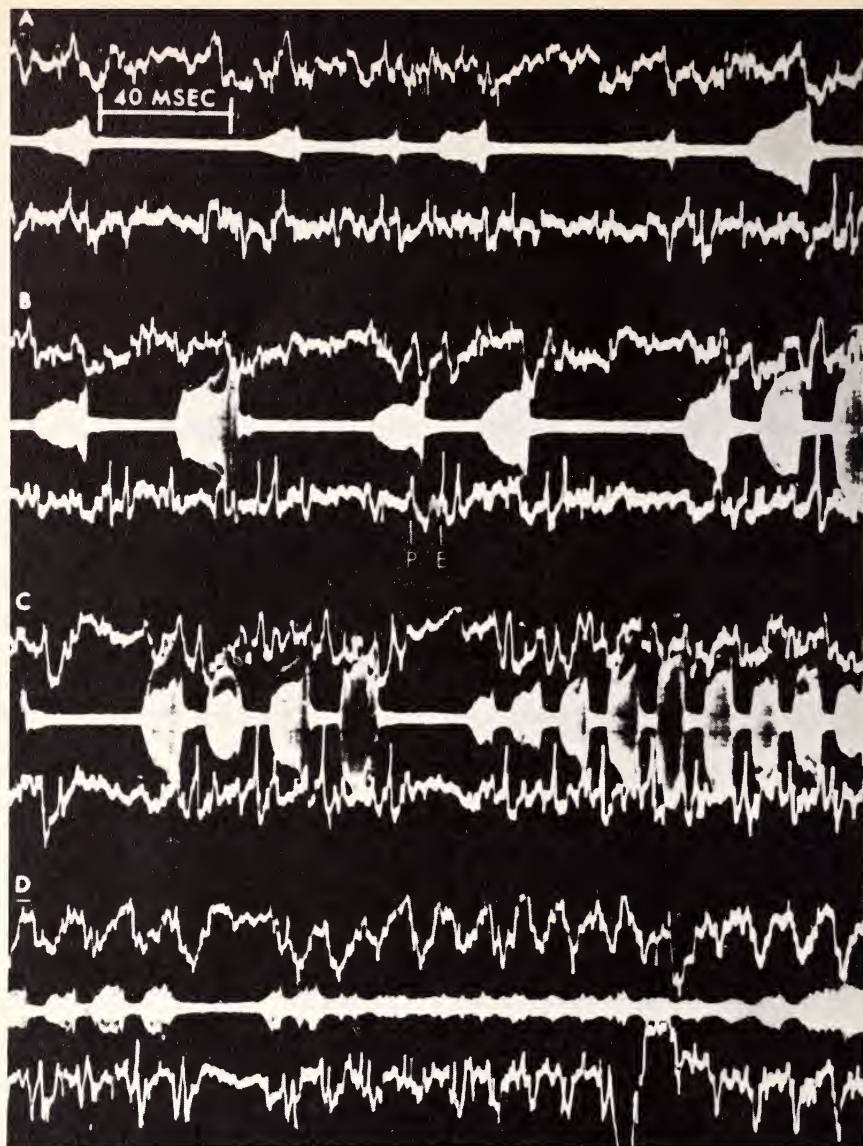


Fig. 11. Collicular evoked response recorded during a typical landing under conditions shown in fig. 6. Upper trace shows potentials recorded from the left inferior colliculus, middle trace shows emitted pulses detected by microphone behind landing area, and lower trace shows right inferior collicular responses. A (pulses 1-6) and B (pulses 7-12) are typical of the search phase. C (pulses 12-25) and D (pulses 26-43) represent the approach and terminal phases of echolocation. The decrease in pulse amplitude during the terminal phase occurred when the animal turned in preparation for landing. The last part of pulse 43 represents the time of landing.

OPERATIONAL PRINCIPLES

It is difficult to determine the amount of pulse suppression. A minimum value of 25 dB has been suggested on the basis of theoretical losses in sonar signal intensities with distance and the equal amplitudes of pulse and echo-evoked CM potentials separated by 6 msec. Minimum values of N_4 suppression may be even higher since echo-evoked responses occurring from 6-15 msec after pulse emission were often much more prominent than the pulse-evoked response (Fig. 11). In the anesthetized animal the difference in stimulus intensity required to evoke a small response as compared to a maximum one was 35 dB or more (Fig. 3).

Several mechanisms may explain the pulse suppression and echo facilitation. Chilonycteris beam their pulses in a forward direction by shaping the mouth like a megaphone; the ears are more sensitive to sounds arriving from the sides than from the midline, and, if favorably oriented, the pinnae seem capable of increasing the sound pressure of echoes at the tympanic membrane relative to that in the free-field. In Tadarida middle ear muscle contractions provide up to 20 dB attenuation of cochlear potentials during pulse emission (31, 32), and they appear to play an important role in pulse suppression and echo perception. The contraction characteristics of these muscles during echolocation are shown in Fig. 12. With pulse repetition rates of 50/sec or less the muscles begin to contract about 10 msec prior to the beginning of an emitted pulse, a maximum state of contraction is reached just as each pulse begins, relaxation ensues over the duration of the pulse and a resting state is reached within 10 msec. With increasing pulse repetition rates less time becomes available for contraction and relaxation between pulses, and at

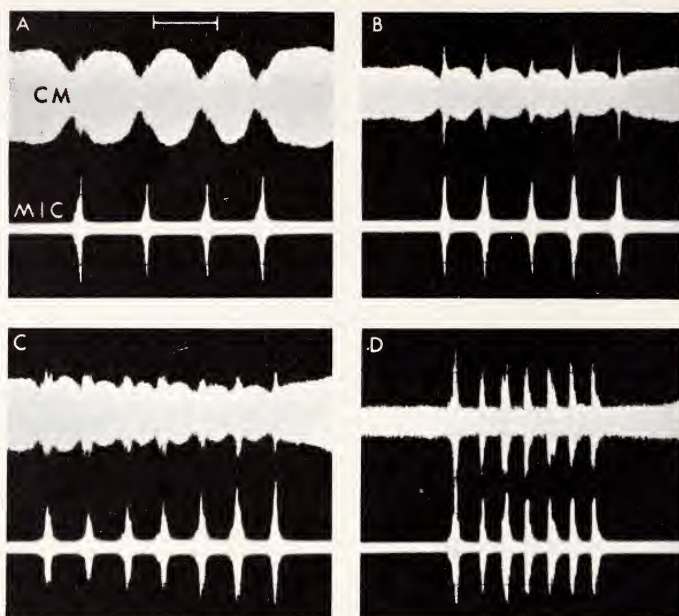


Fig. 12. Middle ear muscle activity associated with pulse emission in *Tadarida*. Cochlear microphonic potentials elicited by continuous pure tone are shown in upper traces. Lower traces show the emitted pulses as detected by a microphone. Prior to the time that each pulse is emitted the middle ear muscles begin to contract and the cochlear potentials are attenuated, a maximum state of contraction is attained as each pulse begins to be emitted and relaxation occurs during pulse emission. Note full contractions and relaxations at pulse repetition rates of 50/sec (A); decreasing contractions and relaxations at 80/sec (B) and 100/sec (C). With pulse repetition rates of 140/sec, the middle ear muscles appear to be tonically contracted while the entire series of pulses is emitted (From Henson (32), by permission Journal of Physiology).

fast pulse repetition rates (140/sec in Tadarida) the muscles appear to remain contracted while an entire series of pulses is emitted. Contractions of these middle ear muscles seem to be synchronized with those of the laryngeal muscles (32, 48). In Chilonycteris the middle ear muscles probably contract during the emission of the pure tone and relax during the terminal FM sweep. By relaxing over a period of 10 msec, or by being tonically contracted during the terminal phase, the middle ear muscles may prevent overstimulation of the ear by loud echoes. The fact that the middle ear muscles contract prior to pulse emission and are not completely relaxed until 4-6 msec after the completion of each pulse indicates that a period of maximum sensitivity exists only during part of the interpulse interval. The duration of this period may be regulated by controlling the interpulse interval; with slow pulse repetition rates and long interpulse intervals, the duration of maximum sensitivity is relatively long and the animals should be able to perceive and evaluate many echoes. By shortening the interpulse intervals the duration of maximum sensitivity is reduced. During the terminal phase when the interpulse interval is short and the muscles are tonically contracted, the system may be 20 dB less sensitive than during other phases. Fast pulse repetition rates and tonic middle ear muscle contractions appear to occur only when the animals are close to their targets and when echoes should be loud. Since middle ear muscle contractions appear to be important for the analysis of loud sounds, the tonic contractions should be beneficial.

There is a close correspondence between the known contraction characteristics of the middle ear muscles and the evoked neural responses

recorded from active bats. The neural potentials recorded from Chilonycteris during the search phase of echolocation showed several distinct echo-evoked responses; during the approach phase only one echo response was seen and during the terminal phase there was evidence of reduced sensitivity. Thus, the results correspond to sensitivity changes that should result from middle ear muscle contractions. In essence it appears that the pulse repetition rate and associated modulations in sensitivity provide a means of controlling the echolocative depth of field.

The macroelectrodes used for studying neural potentials in Chilonycteris recorded the summed responses of many units. It was not possible to say which units produced the response, but inhibitory and facilitory interaction in central auditory pathways could have produced records similar to those observed in flying Chilonycteris. If neural inhibition occurred during pulse emission one would not expect to see marked pulse-evoked responses and high amplitude echo-evoked potentials should have been produced if many units were facilitated by the outgoing cry. Reduced echo sensitivity during the terminal phase may also have been the result of inhibition and incomplete recovery.

The potentials recorded from Chilonycteris raise several questions as to the importance of the pure tone component of the emitted pulses. On the basis of distinct pulse and echo-evoked responses elicited by the FM sweep, the absence of responses to pulse-echo overlap under most conditions, and the apparent echo-masking capacity of the pure tone, it would appear that the FM sweep is the important part of the pulse. It is tempting to

suggest that the pure tone functions as a masking stimulus and thereby assists the middle ear muscles in limiting the echolocative depth of field. On the other hand, Chilonycteris and Rhinolophus emit highly beamed pulses, have isolated cochleae, and often move their head or ears during pulse emission; these features suggest that every effort is made to prevent the outgoing cry from masking the echoes. The pure tone component of Chilonycteris pulses is surely utilized for echolocative purposes, but in what manner remains to be determined.

SUMMARY

Anatomical and physiological studies have shown that the auditory system of bats is basically similar to that of other mammals; it is, however, specialized for ultrasonic perception and the system is highly sensitive to echoes of self-emitted cries. Echo sensitivity is seemingly dependent on mechanisms which suppress sensitivity during signal emission and facilitate the perception of echoes. Neurophysiological evidence suggests that the system operates in the following manner:

1. Prior to pulse emission motor units associated with the laryngeal and middle ear muscles are activated. Contractions begin about 10 msec prior to pulse emission, a maximum state of contraction is reached as pulse emission begins, relaxation occurs during the FM sweep and is completed within 10 msec.
2. The emitted pulses are beamed in a forward direction either through the mouth or nose (depending on the species); this, plus middle ear muscle contractions, the directional

characteristics of the pinnae and cochlear isolation reduce the amount of pulse energy reaching the ear.

3. By reducing the pulse energy the sensitivity of the system is maintained in a relatively high state of sensitivity for the perception of echoes. The majority of collicular units appear to be fully recovered within 6 msec, about twice as fast as that observed in anesthetized bats stimulated by artificial pulses and echoes.
4. The external ears add considerable directionality to the system; depending on their orientation, they may enhance or reduce the energy of acoustic signals reaching the ear. Large differences in sound pressure may occur binaurally and these differences appear to permit accurate sound localization.
5. In bats which emit pulses of long duration ear and head movements occur and it is suggested that these modulate the acoustic input, perhaps shifting the balance between masking and unmasking in relation to the pure tone component of the pulse. In these bats, however, the important part of the pulse is a terminal FM sweep.
6. The bat's ear is maximally sensitive only during the interval between pulses. By controlling the pulse repetition rate bats appear to limit the echolocative depth of field and focus their attention on a primary target.

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ABSTRACT

Cochlear microphonic and evoked neural potentials recorded from Tadarida and Chilonycteris indicate that the efficiency of the bat's sonar system is highly dependent on a complicated interplay between peripheral and central auditory mechanisms. In flying bats there was evidence of marked pulse suppression at both peripheral and central levels; the amplitude of collicular (N_4) responses evoked by emitted pulses was usually small in comparison with echo-evoked potentials. Forward beaming of the emitted pulses, the directional characteristics of the external ears, and middle ear muscle contractions seem to play an important role in both pulse suppression and echo perception. Neurophysiological evidence suggests that bats limit the echolocative depth of field by controlling the pulse repetition rate and interpulse interval. In bats which emit long pure tone pulses terminated by an FM sweep, the FM sweep appears to be the important part of the pulse; it is the only part which normally evoked distinct neural responses to echoes.

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DISCUSSION

by
N. SUGA

An introduction to auditory physiology in bats and its recent advances was presented by O. W. Henson. Of special interest in his presentation is that the neural activity evoked by echoes is larger than that evoked by outgoing orientation sounds, even when the echo delay is as much as 15 msec. As a discussant, I would like to comment on this presentation on the basis of single neuron analysis which concerns echo-reception in bats. Most data in this comment are based on the experiments performed in collaboration with J. H. Friend and R. A. Suthers (4).

O. W. Henson (5) has shown that sound-evoked potential changes, consisting of four fast-positive and one slow-negative, are recorded with an electrode placed on the inferior colliculus. He also illustrated that the fourth positive component was the summated activity of the input of the inferior colliculus, and the slow one, that of the collicular neurons. To explore the functional properties of single neurons, we inserted a microelectrode with a tip diameter less than 0.3μ into the inferior colliculus of an anesthetized bat (Myotis lucifugus). Incoming fibers from the auditory nuclei that were lower than the colliculus were avoided. That is, we studied the neurons in the level higher than those described by O. W. Henson. In the auditory system, there are many relay nuclei in which tonal information is processed step-by-step. The inferior colliculus of echo-locating bats is hypertrophied. It is highly probable that the properties of electrical activities in the

incoming fibers to the colliculus and the collicular neurons differ from the outgoing fibers from the colliculus. If there are differences, they may provide clues to the neural mechanism of sensory processing in the colliculus.

The transducer in the cochlea changes sound energy into bioelectric potential. This potential, called "cochlear microphonics," follows the wave form and character of a tonal stimulus conducted into the inner ear through the oval window. In the transducer, there is neither refractory period nor adaptation; while the auditory nerve fibers show a short refractory period and slow adaptation, in general. Therefore, there is a limitation in following of nerve impulses to sound waves. Davis (2) noted that impulses of the auditory nerve fibers were synchronized with the stimulus waves at 2 KH_3 and 4 KH_3 . Tasaki's review (15) states that with low frequency tones, the action potentials of single fibers show a clear tendency to appear at a definite phase of the applied sound wave. This tendency is obscure for frequencies higher than 2 KH_3 . Katsuki et al (8) reported a cochlear nerve fiber which showed a maximum discharge rate of over 800 impulses per second. Peake et al (9) detected auditory nerve responses synchronizing with short noise bursts at repetition rates as high as 3000 per second. Furthermore, Rose et al (11) described a cat's collicular unit with an input having a phase relation with sound waves of up to 2.86 KH_3 . In bats, many auditory nerve fibers and cochlear nuclear neurons began to

recover in 0.6-0.7 msec after the response to the 1st tone pulse. Full recovery occurred in 1-3 msec. The rate of impulse discharges usually increases to more than 300 per second. The data indicate that the peripheral neurons can be fired by two sounds, closely spaced in time. However, there are many psychological and evoked-potential studies that demonstrate the post-stimulation depression of sensitivity. Why does the evoked-potential study show the slow recovery of N_1 , in spite of both the absence of a refractory period in cochlear microphonics and a high discharge rate of the peripheral auditory neurones?

In general, neurons in the cochlear nerve fibers show tonic responses and monotonic spike-count functions (monotonic increase in the number of impulses with stimulus intensity) for a wide intensity range. When a short, strong tone pulse is delivered, the neuron usually discharges a few (or a train of) impulses. This probably causes the slow recovery of N_1 . How, then, does the neuron code the difference between a strong single-tone pulse and a few (or a train of) weak-tone pulses that are closely spaced? How does the neuron detect a weak sound delivered during a train of impulses caused by a strong tone pulse? Peripheral neurons do have recovery cycles which are short enough to fire for echoes coming back immediately following the outgoing pulse. However, those neurons are not good enough for echo-detection and ranging.

To improve this, the auditory system seems to possess

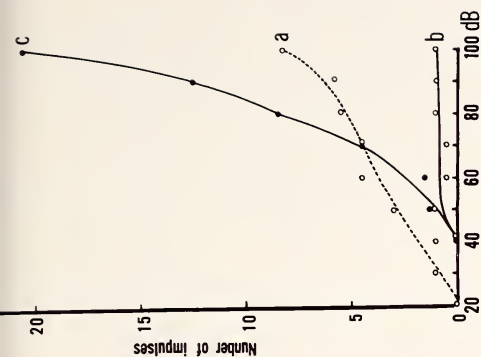


Fig. 2.

Change in the number of impulses (ordinate) in the central auditory neurons (called T large fibers) of a grasshopper before (b) and after (c) eliminating the inhibitory effect by cutting the contralateral tympanic nerve. The abscissa represents the intensity of a 17 KHz sound (dB re. 0.0002 dyne/cm²). A loudspeaker is placed to the left side of an insect. The left T large fiber (a) sends more impulses than the right (b). When the left tympanic nerve is cut, the left T large fiber stops impulse discharges, while the right sends the increased number of impulses (c). (From N. Suga, & Y. Katsuki, 1961.)

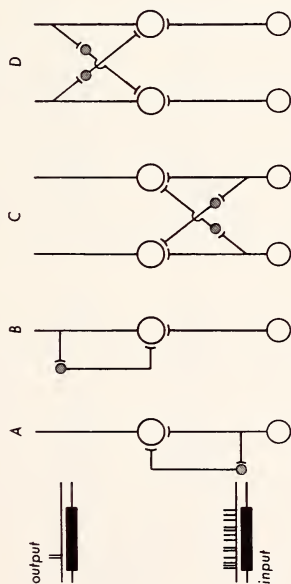


Fig. 1.

Four basic neural networks to change a tonic response and short recovery cycle into a phasic response and recovery cycle with various durations. Open circles show excitatory neurons and shaded circles, inhibitory interneurons.

The excitatory neurons at the bottom send impulses during a stimulus, while the upper excitatory neurons discharge impulses only at the onset of the stimulus because of the delayed arrival of the inhibitory bombardment.

both muscular and neural mechanisms. The effect of muscular control on self-stimulation caused by outgoing orientation sounds, i.e., suppression, was demonstrated by O. W. Henson (7). As the neural mechanism, augmentation (6) and suppression (4 and 12) are conceivable. In the examination of a response pattern of peripheral auditory neurons, suppression of impulse discharges seems to be one way to improve echo-detection and ranging. If so, there may be at least two ways by which the auditory system, using inhibitory neurons, can act, i.e., by changing both response pattern and recovery cycles of neurons. If the response pattern changes from tonic to phasic to discharge only one impulse per tone pulse, the echo-detection and ranging may be improved. This improvement may be made if the duration of the recovery cycle of a neuron changes in order to require a certain period of time to fire again after the response to the outgoing pulse. The changes in response pattern and recovery cycle do not require special neural networks. Figure 1 shows four networks which have been proposed and identified many times by physiologists, psychologists and anatomists. These networks can change the response pattern and recovery cycle.

When microelectrodes are inserted into the inferior colliculus, one can easily find neurons which show phasic responses and short or long recovery cycles. Most neurons discharge a few impulses for a tone pulse, but some respond with only one impulse to sounds in a wide intensity range.

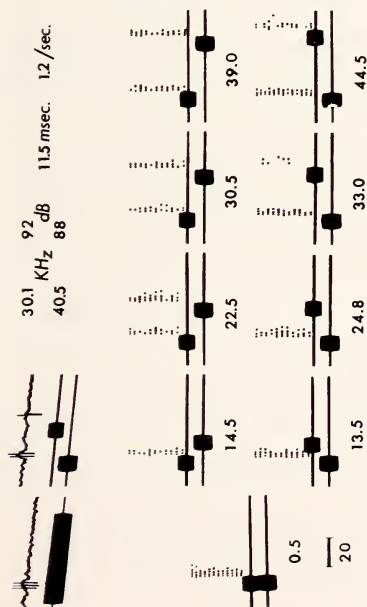


Fig. 3.

Recovery cycle of an inferior collicular neuron after on responses to tone pulses with different frequencies. Tone pulse I is 30.1 KHz, 92 dB, and II is 40.5 KHz, 88 dB. Their durations are 11.5 msec. The repetition rate for the pairs of pulses is 1.2/sec. Impulses as shown in the uppermost photographs are presented in the other photographs by a dotted pattern, in which one dot corresponds to one impulse. The figures under each photograph show the interval between the onsets of the tone pulses in milliseconds. See text. (From N. Suga, 1964.)

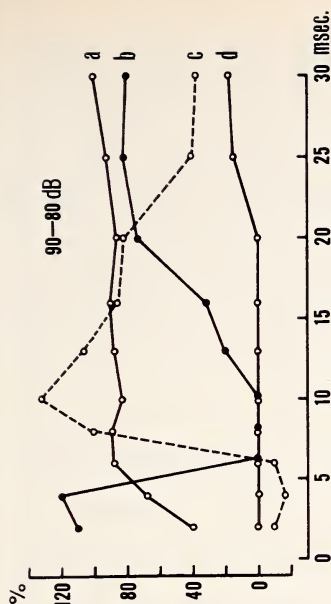


Fig. 4.

Four types of recovery cycles in the inferior colliculus. (a) short suppression, (b) delayed inhibition, (c) temporary recovery, and (d) undelayed inhibition. These were measured in four single neurons with a pair of FM tone pulses, the first 90 dB, the second 80 dB. The ordinate represents the response, and the abscissa, the interval between the onsets of the first and second tone pulses in milliseconds.

100% response corresponds to the number of impulses per second tone pulse when it was delivered alone. In these examples, this value was 1.00 for a, 2.75 for b, 1.28 for c, and 1.58 for d. (From J. H. Friend, N. Suga & R. A. Suthers, 1966.)

In Fig. 2 (14) the central auditory neuron of a grasshopper is presented as the simplest example in which a flat spike-count function is produced by inhibition in the auditory system. This central neuron receives excitatory bombardments from the ipsilateral tympanic nerve, and inhibitory bombardments from the contralateral nerve. The central neuron shows a monotonic spike-count function without inhibitory input (c) but a flat spike-count function with it (b).

The recovery cycle has been customarily measured with a pair of stimuli. For example, a neuron in Fig. 3 (upper photographs) shows a phasic response to a pure tone pulse. In the other photographs, nerve impulses are shown by dots. The neuron discharged 2.0 impulses on the average to tone pulse I and 2.7 impulses to tone pulse II. When tone pulse II was delivered after tone pulse I, the response to tone pulse II was inhibited at a 14.5 msec delay, but recovered at a 22.5 msec delay (middle row). Whereas the response to tone pulse I following tone pulse II was inhibited at delays of 13.5 and 24.8 msec, the response began to appear at a 33.0 msec delay (bottom row). Since the recovery cycles are the function of frequency and intensity of the 1st and 2nd tone pulses, it is difficult to classify them clearly. For convenience, therefore, they are categorized into four groups: (1) short suppression (a in Fig. 4), (2) delayed inhibition (b in Fig. 4), (3) temporary recovery (c in Fig. 4), and (4) undelayed inhibition (d in Fig. 4). A pair of FM tone

pulses, which were the same in duration and frequency but which could be varied in intensity, were spaced at various interval to imitate a bat's orientation sounds and echoes. In the inferior colliculus, 144 recovery cycles were studied and categorized into these four groups. Only 4% showed short suppression; 11%, delayed inhibition; 7%, temporary recovery; 78%, undelayed inhibition. The duration of the inhibitory period differed from neuron to neuron. In total, about 96% of the neurons had inhibitory periods. It is clear that the brain does not work with the averaged activity of neurons. Therefore, the problem may be discussed as follows: Four per cent of the neurons with short recovery cycles are the most suitable for echo-detection and ranging. Seven per cent of the neurons which show temporary recoveries are the most suitable for the detection of echoes coming back in certain periods of time. Then what does the majority of neurons with inhibitory periods do? They should not be redundant channels in echo-detection and ranging, because 30% of such neurons seemed to be specialized for the analysis of complex sounds (13).

The recovery cycles of collicular units depended on the intensity, frequency, and duration of the 1st and 2nd tone pulses (Fig. 6), and there was considerable variation between units in the duration of the inhibitory period. This spectrum of recovery, as well as the phasic response pattern that is

favorable to echo-detection and ranging, might provide a mechanism for discriminating between echoes from objects at different distances.

Let us compare two systems. In one system, all neurons have such a short recovery cycle that they can respond to all echoes coming from objects at various places. When the distance between a bat and a target is shortening, the number of neurons activated by the echoes increases rapidly with the increasing intensity on this system. Echoes coming from objects at different distances are processed by the same group of neurons in terms of recovery cycle. In other words, it may be said that the greatly increased number of neurons at the higher level of the auditory system has less meaning in differentiation for temporal analysis. In the other system, in which neurons differ from one another in the recovery rate, the number of activated neurons may not increase or may remain constant during the approach to the object. In other words, when the distance between the bat and the object is short and the echo intensity is strong, the number of neurons activated is decreased by an inhibitory effect. When the distance is long and echo intensity is weak, many neurons are released from inhibition. This compensation is suggested on the basis of the measurement of recovery cycles at the highest level of the auditory system.

Since the number of collicular units activated by the 2nd tone pulse decreases with the interval between tone pulses,

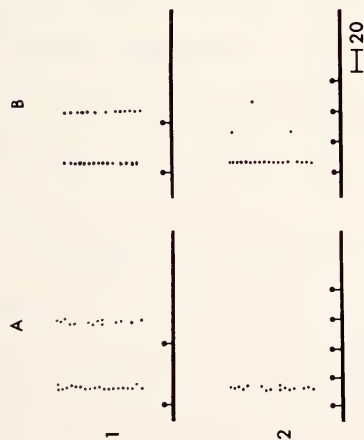


Fig. 5.
Responses of two single neurons (A and B) to repetitive stimuli with click sounds. Nerve impulses are shown by a dotted pattern as in Fig. 3. In 1, the minimum intervals for the recovery of the response to the second click are shown. In 2, click sounds in a series are spaced at the maximum interval for the for the complete inhibition of the response to the second click. The time scale is 20 msec. See text. (From J. H. Friend, N. Suga & R. A. Suthers, 1966.)

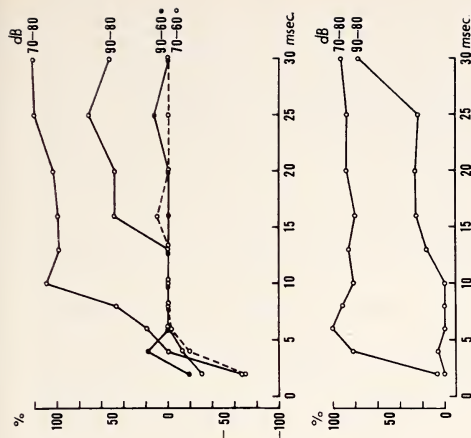


Fig. 6.
Recovery cycles of two single neurons, A and B, showing the effect of relative intensities of tone pulses. The intensity of a pair of FM tone pulses is shown to the right of each curve (e.g., 70-80 means the first tone pulse was 70 dB, and second, 80 dB). In A, +100% responses signifies that the second pulse produced as many impulses as when delivered alone; 0 means only the response to the first pulse; and negative values mean that even the response to the first pulse was reduced by the percentage indicated. (From J. H. Friend, N. Suga & R. A. Suthers, 1966.)

there is a possibility that the inferior colliculus is necessary to analyze echoes from objects in the search and probably in early approach phases, but not in the terminal phase in object-avoidance or insect-catching. Figure 5 shows responses to repetitive click stimuli of two collicular neurons with undelayed inhibitory periods. First, the recovery cycle of an unit was measured with a pair of clicks of the same intensity. In Fig. 5, 1, the interval for 100% recovery is shown. Next, the interval between the clicks was set to the period of complete inhibition. Finally, the number of clicks in the series was increased one by one until the total length of the series exceeded the interval for the complete recovery. However, a response only to the 1st click of each series was observed (Fig. 5, 2). It is explicit that the inhibitory period caused by each of the clicks overlapped, whether or not each click produced nerve impulses. This result suggests that the collicular neurons with inhibitory periods do not respond to echoes during the terminal phase of obstacle-avoidance or insect-catching and that the neurons are prevented from sending erroneous information.

In the olivary complex (the 2nd relay nucleus), binaural interaction first occurs and fibers for acoustic reflexes originate to connect with the motor nuclei of the muscles of the eyes, middle ear, face, neck, and body (1). Many neurons

in this nucleus can probably respond to both the outgoing pulses and to the echoes from short distances, since the input of the inferior colliculus, i.e., fibers ascending from both the cochlear nucleus and olivary nuclei to the inferior colliculus through the lateral lemniscus, have short recovery cycles (6). In cats and rats, the most fundamental analysis of sound, i.e., intensity discrimination, is possible at the level of the olivary complex (10 and 3). Therefore, it is possible that the information a bat needs for short range echo-location is processed by the bulbar auditory nuclei. The inferior colliculus seems concerned with echoes in cruising and probably early-approaching phases and seems to analyze and discriminate minor differences among echoes (4 and 13).

Validation of this illustration was examined by observing behavior of a bat after the bilateral ablation of the inferior colliculus, where single-unit activities were recorded. The bats (Myotis yumanensis) were anesthetized with Nembutal, and both of the inferior colliculi were ablated. Both eyes were closed with sticky wax. After the operation, the bat showed normal landing and avoidance from a hand or an insect net thrust up across the flight path. Orientation sounds were produced during the flight. One bat sometimes hit a wooden bar 6 mm in diameter. Although the brains of these bats were not histologically examined, about 70% or more of the inferior colliculus was probably ablated. The evoked potential of the

ablated inferior colliculus showed the fast component (N_4) in a small amplitude, but not the slow one. These results show that the loss of a majority of collicular neurons with long recovery cycles did not impair landing and avoiding a large object, but the acuity may be poor to some extent.

O. W. Henson showed that the attenuation of self-stimulation caused by the outgoing pulse improved the detection of echoes. This is also easily demonstrated by the measurement of the recovery cycle of a single unit. Two examples are shown in Fig. 6. In A, FM tone pulses swept from 60 to 30 KH_z during a 2 msec duration. When an 80 dB FM tone pulse was delivered 2 msec after a 90 dB pulse, the neuron showed no response to the 2nd pulse, and firing rate to the first decreased by 21% (curve 90-80). The response to the 2nd pulse began to recover between 13 and 16 msec. When the first pulse was attenuated to 20 dB, however, the change in the recovery cycle was drastic (curve 70-80). The response to the 2nd tone pulse began to recover at 6 msec. On the other hand, 20 dB attenuation of the 2nd tone pulse increased the length of the recovery cycle, even if the neuron discharged more impulses to the 60 dB sound than to the 80 dB (curve 90-60). A 40 dB tone pulse, which did not excite this neuron, remained ineffective when delivered as the 2nd tone pulse after a 90 or 70 dB pulse. In B, another example is shown in which 20 dB

attenuation of the 1st tone pulse drastically shortened the recovery cycle. Fifty per cent recovery occurred at 27.2 msec when the 1st tone pulse was 90 dB (curve 90-80) and at 3.1 msec when the 1st was 70 dB (curve 70-80). Shortening of the recovery cycle with a weaker 1st tone pulse was usually seen, irrespective of the intensity of the 2nd tone pulse.

The extent to which the data obtained from the anesthetized animal is applicable to the brain of the unanesthetized animal is always a problem. Probably only the most static properties of neurons are studied in the anesthetized animal. The most dynamic properties of neurons which act under many feedback systems may be found only in the awake animal. The experiments along the lines of O. W. Henson's work will explore the dynamic state of the brain of echolocating bats.

SUMMARY

Single neurons in the cochlear nucleus showed tonic responses to tonal stimuli. The recovery cycles of the responses were so short that the neurons were excited by echoes coming back within a few milliseconds after an outgoing orientation sound. However, these neurons were not suitable for echo-detection and ranging, since they usually discharged a train of impulses for a strong tone pulse and had difficulty in distinguishing a single strong

tone pulse from a train of weak ones. Neural inhibition in the central nervous system changed the response pattern and recovery cycle and seemed to improve the ability of echo-detection and ranging. The role of the inferior collicular neurons with inhibitory periods was discussed.

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ABSTRACT

Echo-reception by single neurons in the inferior colliculus of echo-locating bats. Nobuo Suga, Department of Neurosciences, University of California, San Diego, La Jolla, California, U.S.A.

Single neurons in the cochlear nucleus showed tonic responses to tonal stimuli. The recovery cycles of the responses were so short that the neurons were excited by echoes coming back within a few milliseconds after an out-going orientation sound. However, these neurons were not suitable for echo-detection and ranging, since they usually discharged a train of impulses for a strong tone pulse and had difficulty in distinguishing a single strong tone pulse from a train of weak ones. Neural inhibition in the central nervous system changed the response pattern and recovery cycle and seemed to improve the ability of echo-detection and ranging.

In the inferior colliculus, neurons showed phasic responses in general; and some discharged only one impulse per stimulus, irrespective of sound intensity. Such a response pattern was probably most suitable for echo-detection and ranging. The recovery cycles of collicular units were classified into four groups: (1) short suppression, (2) delayed inhibition, (3) temporary recovery, and (4) undelayed inhibition. Most neurons showed inhibition immediately following an on response. The duration of inhibition differed from neuron to neuron. This variety in the recovery cycle may provide a mechanism for discriminating echoes from objects at different distances. The role of the inferior colliculus was discussed.

cochlear nucleus, echo-reception, inferior colliculus, recovery cycle.

DISCUSSION
by
O.W. HENSON Jr.

Dr. Suga's experiments with single units in Myotis and my experiments with evoked responses in Chilonycteris are in agreement with respect to periods of neural inhibition following stimulation of the ear in anesthetized bats. On the basis of responses recorded from Chilonycteris performing landing maneuvers, it seems likely that this inhibition occurs under natural conditions; however there is sufficient evidence from the records to suggest that the period of inhibition is much less under natural conditions than under artificial ones.

The real question is the meaning of this inhibition. While Dr. Suga suggests that it may be utilized for range determination, I think there are several points which argue against this interpretation. (1) The variable periods of inhibition described for collicular units in bats do not differ significantly from those of non-echolocating animals. (2) The period of inhibition and the subsequent responsiveness of neural units are dependent on the intensity of pulses and echoes reaching the ear; both must vary considerably under natural conditions, not only from pulse to pulse, but also from target to target and time to time. I favor the interpretation that this inhibition serves to sharpen the image of the primary echo source or target. Since returning echoes rather than the emitted pulses cause a high degree of neural excitation, many collicular units should be inhibited following echo stimulation. Such inhibition could certainly focus the system on the first echo returning to the ears and make it relatively insensitive to following echoes. The same thing could be accomplished by simply increasing the pulse repetition rate as described in the main text of my report.

DISCUSSION

by

L. KAY

This paper is directly related to some of my early thoughts on the sonar system of the bat (35). These arose entirely from the system I envisaged as being particularly suitable for blind persons and which is presented elsewhere in these proceedings. Some new ideas had arisen which I felt may have some relevance to bat sonar, since at that time (1959) little was known about it outside the small groups actively engaged in this field. I was intrigued to learn on reading Griffin's book (15), that questions were being asked about the frequency-sweep used by many bats, because this was similar to what I believed was the best form of coding of the radiated energy for coupling to the human auditory system. The basis for my hypothesis in (35) was therefore in no way related to behavioural studies of bats, and it would be remarkable if my suggestions were substantiated by experimental evidence. Pye (56) had similar ideas, quite independently, at about the same time; these undoubtedly were directly related to the behaviour of the bat. We both wished to stimulate further thought on the subject, and whilst many others have also contributed similarly, I am sure that - judging from the paper under discussion - our effort was not entirely wasted. It is very interesting now to be able to look back over later developments and, in particular, to have this opportunity to discuss results of research of a highly related nature.

Dr. Henson has presented some very useful data on the bat sonar system and is to be congratulated on his neurological experiments, the results of which correlate closely with behavioural evidence and communication theory. Neurophysiological experiments still involve the gathering of coarse data from which finely graded hypotheses must be drawn. Gross errors are possible and it is only by linking various sources of evidence together

that one can gain confidence in new information.

There is - so far as I am aware - no confirmatory data published on the importance of the F.M. Sweep used by Rhinolophus and Chilonycteris. Some experiments carried out by Griffin and me in 1961, however, are now seen to be relevant, although at the time in isolation we did not think that publication was justified. We were attempting to mask the sonar of two Greater Horseshoe bats by directing high level wide band noise at their ears when perched and in flight. We also attempted to mask the tone transmission of the bats by radiating tone of exactly the same frequency (as far as was possible). All we appeared to do was disturb them. When the noise field was switched on there was a clearly noticeable reaction. The duration of the pulses was greatly reduced and the repetition rate increased. In addition, the terminal frequency-sweep became more marked. Under normal conditions the pulse duration would be up to 60 ms and the terminal change in frequency relatively small compared with the Vespertilionidae family. The repetition rate was leisurely. Immediately the noise field was present, the frequency-sweep would increase to 20-30 kHz/s and the sweep duration would be of the order of 2 ms. It was also of greater intensity. The tonal frequency remained constant at about 80 kHz/s. When the tone field was switched on there was little reaction observed; occasionally a similar reaction to that for noise would be observed, but we could not be sure that this was not due to other causes. For example, movement of the hands in front of the bats produced reactions similar to those caused by noise.

My conclusion was that the F.M. waves carried most of the information and since the noise was masking this, both the bandwidth and the intensity had to be increased. The tone did not mask the environment and therefore did not disturb in the same way. These results are now seen to correlate with Henson's results.

Communication theory leads us to expect little information about the environment from long tone transmissions other than changes in the environment which produce a Doppler shift of frequency. Environmental detail which is being masked by noise can be obtained only by the use of a wide frequency band..

I made mention, earlier, of the coding of the emission. A general theory of the sonar system does not specify the coding of the signal; this can be in various forms (pulses of tone, random waveform, F.M. Sweep, etc.), but it is essential that the returning echoes be correlated with the emission if range detail is to be obtained. Correlation infers the existence of a memory which stores the original code. This was taken into account when I first discussed the sonar system of the bat. If no correlation takes place the system is no more effective than a passive system-even though it appears active. The frequency sweep appeared attractive in this respect and it also matches the auditory input more than very short tonal pulses of comparable bandwidth ($20\mu s$). Both Pye and I thought of beat notes, but this is not the only way in which correlation may be obtained. The emission will produce firing of the hair cells in sequence along the basilar membrane and the pattern of impulses will be stored for some time in neural pathways (up to 15 ms (20) (21)). Echoes will each produce similar patterns which will travel along the same complex of pathways. Following models by Grinnell and Sayers-Cherry, it requires little imagination to see the possibility of both running cross and auto correlations taking place at different levels.

Grinnell (23) suggests that interaural time differences are less important than amplitude differences and this is supported by Konstantinov (36). Their evidence leads one to believe that the mechanism is different for humans and therefore comparisons should not be made. If this is in fact so, comparison

between Grinnell's model and that of Sayers and Cherry is not valid. I do not find this evidence sufficiently convincing however. Experiments with humans on normal auditory perception, on which some of their evidence is based, may be inadequate and the importance of interaural time differences in bats cannot be adequately assessed by the experiments so far conducted, since the data is too coarse. Recent experiments at Canterbury using humans with ultrasonically aided auditory perception are showing that interaural amplitude difference is an important localization cue in humans too. Time differences may be of less importance but at this stage I am not prepared to commit myself. I would only point out that our evidence may not conflict with Grinnell's.

A feature not mentioned is the interaural frequency-difference. Little appears to have been said about this in the literature. There is a big difference here between the bat and the ultrasonically aided human. In the bat the pattern in each ear is the same - displaced in time. In the human the difference is not a function of time at the ears, although a time-difference produces the effect. In consequence experiments cannot be carried out with humans which may easily be related to the bat's F.M. features.

Dr. Henson's summary of the sonar system is thus supported by some other evidence, but the conclusion which I find the weakest is the great importance placed on amplitude differences. This may well turn out to be the case, but more must still be done in this area particularly as it has an important bearing on the processing of signals.

DISCUSSION

by

A. D. GRINNELL

I would like to voice my great admiration for Dr. Henson's work, and make but two or three short comments. His experiments are a beautiful fulfillment of what must be an objective of all of us who study neural correlates of behavior: the extraction of data during apparently normal behavior. I know how difficult this is.

Despite this difficulty, I wonder whether it would not be possible to denervate the nerves supplying the middle ear muscles, in Chilonycteris or in any other bat known to use their muscles in the way Dr. Henson has shown. This would provide another assessment of how important this peripheral blanking-out mechanism is, how important any central mechanism might be, and how the bats might compensate for the change. Would this be possible? (I'm tempted to try it myself.)

I would like to come to the defense of Chilonycteris, or perhaps of evolution, on the question of their frequency resolution. Collicular responses in the Chilonycteris I studied in Panama were masked with about the same effectiveness by tones of near-by frequencies as are the equivalent responses in Myotis or Plecotus. I am quite convinced their ability to discriminate frequencies is no less. A much larger portion of the auditory system does seem to be tuned to a fairly narrow band, especially in the off-response, but this is a different phenomenon.

Finally, with respect to what seems to me to be the most intriguing thought in the paper---the possible role of the constant wavelength (CW) part of the Chilonycteris pulse as a "focusing" device, arranged to mask out unwanted echoes, I am full of doubts. What about the other echoes that might be important, even at a greater delay? And is the clutter of

later echoes likely to be more disabling than the louder CW signal that clearly masks them? Since it does mask these later echoes, can it really be expected that it will interfere less with the earlier echo than the masked echoes would? Maybe so. I really distrust my intuition here, but it tells me that a bat would be better off with only the FM portion of the pulse, if the role of the CW part was only "self-masking." It seems much more likely, to me, that that CW portion is used to obtain Doppler information or for direction determination.

DISCUSSION

par

J. C. LEVY

L'exposé du Dr. HENSON montre d'une façon saisissante la similitude qui existe entre les radars créés par l'homme et les sonars dont la nature a doté les chauves-souris.

Il s'agit là d'un travail de "Bionique" dans la plus complète acceptation du terme, à cela près que les ingénieurs avaient inventé le radar avant que ne soient aussi bien connus les organes de chauve-souris.

Moyennant le fait que le radar utilise les ondes électromagnétiques et le sonar des chauves-souris des ondes ultra sonores, on peut retrouver dans la chauve-souris les principaux éléments constitutifs du radar.

Nous dirons que les principes de ces deux instruments sont similaires, seule diffère la réalisation technologique.

On y retrouve:

- Radar à impulsions ou radar à modulation de fréquence (Chilonycteris).

L'oreille externe représente l'aérien; le mécanisme de l'oreille moyenne réalisant l'adaptation d'impédance entre l'aérien et le récepteur.

Le système récepteur possède sa propre bande passante, l'opération est réalisée par les muscles de l'oreille moyenne, mais le système de la chauve-souris est ici plus complexe que celui du radar dans lequel la bande passante est déterminée par la géométrie de l'antenne et de ses circuits d'adaptation, il n'y a pas de modification de ces derniers par action des circuits électroniques du récepteur.

Les dispositifs de protection de l'oreille contre les chocs acoustiques correspondent aux dispositifs anti TR des radars.

L'oreille interne correspond aux étages haute et moyenne fréquence des récepteurs. Noter sa protection par couche de graisse contre les vibrations osseuses, qui en technologie électronique serait remplacée par un blindage des filtres de protection d'alimentation etc.

Les circuits nerveux placés après l'oreille interne constituent les circuits video. L'on sait faire des circuits video qui possèdent des "fenêtres" permettant de ne recevoir que les échos correspondant aux distances utiles; le même mécanisme a été mis en évidence chez la chauve-souris.

Signalons enfin que l'aller et retour des pavillons de l'oreille du Rhinolophus doit correspondre à l'opération appelée "Bilobing" destinée à améliorer la précision de la mesure de direction.

Ce dont nous ne voyons pas l'équivalent chez la chauve-souris, ce sont les indicateurs visuels qui n'existent certainement pas. Si nous assimilons le sonar de la chauve-souris à un radar, nous ne pourrions trouver que le radar dont les indications sont directement utilisées pour commander un instrument.

C'est-à-dire qu'il reste à comprendre comment la chauve-souris "intègre à un niveau supérieur" les indications fournies par son sonar pour aboutir à des réactions motrices appropriées.

J'ignore ce qui a été fait dans ce domaine, mais personnellement je pense que nous en sommes réduits aux conjectures.

REMARQUE

Il a été signalé par HENSON que l'analyse de fréquence de "Myotis" se fait en un temps de 0,2 milli seconde.

Il existe à ce sujet une théorie due au mathématicien GABOR d'après laquelle le produit de l'erreur admissible en fréquence par la durée de cette mesure ne peut pas tomber en-dessous une certaine valeur.

Autrement dit, la précision de mesure de fréquence ne pourrait être, dans ce cas, que de $\pm 1,25$ kHz.

Il est possible de tourner la difficulté si le signal est beaucoup plus puissant que le bruit de fond.

Il est difficile d'exprimer mathématiquement l'intensité du signal parvenant aux circuits nerveux, et de le comparer au bruit de fond dû au bruit ambiant, aux bruits organiques de l'animal (circulation du sang) et au bruit neural.

L'on peut supposer que le bruit interne correspond au bruit ambiant multiplié par un certain coefficient que l'on appelle "facteur de bruit". Ce facteur tient compte du bruit propre à l'organisme de l'animal ajouté au bruit ambiant.

Dans ces conditions l'on peut exprimer le signal S et le bruit B par des grandeurs physiques de même nature qui sont des pressions de vibration.

Dans ces conditions la précision peut être calculée à partir de la formule de HARTLEY et du théorème de SHANNON.

Je ne préciserai pas les formules qui seraient trop sujettes à discussion, compte tenu du manque de précision relatif aux hypothèses de départ.

Toutefois, il sera toujours utile de s'assurer que les performances réalisées par les animaux sont conformes à la théorie physique.

Ce point sera encore discuté dans ma contribution à la discussion générale qui a pour sujet: le traitement de l'information dans les systèmes biologiques.



IX

Les théories des systèmes sonars
et leurs applications
aux organismes biologiques

Theories of sonar systems
and their application
to biological organisms



THEORIES OF SONAR SYSTEMS AND THEIR APPLICATION TO BIOLOGICAL ORGANISMS

by
Dwight W. BATTEAU

Perhaps the earliest indications of sonar were provided simply by listening. Animals could be recognized by the sounds they made, not only vocally, but in movement. Grass and trees are easily heard when the wind blows. The sound of a shore, of rocks or sand or reefs, is well characterized by the sound produced by waves that wash there. And the sounds of rain and storm and hurricane are unmistakable. However, these natural sounds, easily distinguished, are presently the most difficult to comprehend by means other than naturally evolved hearing.

The next instance of the use of sonar may be provided by the natural echo such as heard from a distant rock wall or between hard surfaces as in mountains where sound reflection is clear. It is easy to form the hypothesis that the time between a sound and its echo indicates the distance of the echo forming structure. The clanging bells of buoys, the fog horns of ships, both provide characterizing signals to indicate the shore features and their location relative to vessels navigating in dark or fog. Here the idea may have been born that active sonar could be used to find the distance, and possibly the character, of objects and environmental features.

When we observe natural acoustical phenomena, it is easy to arrive at the idea that a sound may be used actively to probe an environment and, since we wish certainty, perhaps we consider that such sounds should be separable from other environmental sounds. This could lead to the theory that very narrow band pure tones would be ideal for active sonar. This is an easy idea, but animals, such as dolphins and bats, do not do this, so perhaps some modification may be necessary upon careful examination.

With this as a beginning, the simplest theory of sonar relates the speed of sound to the distance of a reflector or echo producing object, by equation (1):

$$2d = tc \quad (1)$$

d = distance of sound source from reflector
 t = time between initiation and receipt of the echo
 c = velocity of sound in the medium.

Since this expression gives no information about the kind of signal being used, it is more appropriate to write equation (2):

$$R(t) = aP(t - \frac{2d}{c}) \quad (2)$$

$R(t)$ = received signal
 $P(t)$ = transmitted signal
 a = attenuation of the transmitted signal
 d = distance of reflecting object
 c = velocity of sound in the medium.

The expression (2) indicates only one reflector, which would be unusual, so that modification (3) is desirable:

$$R(t) = \sum_{n=1}^{\infty} a_n P(t - \frac{2d_n}{c}) \quad (3)$$

a_n = an attenuation associated with the n^{th} reflection.

In (3) an attenuation coefficient is assigned to each reflecting object corresponding to each distance. In most cases, there will be some back-scatter from the medium, so that a continuous reflection may be necessary for characterization, as in (4).

$$R(t) = \int_0^{\infty} a(\tau) P(t - \tau) d\tau \quad (4)$$

$$\tau = \frac{2d}{c} \text{ for all } d$$

$a(\tau)$ = an attenuation associated with the corresponding distance of delay .

Equation (4) may be recognized as an integral transformation of $a(\tau)$ by the kernel $P(t - \tau) d\tau$. If the inverse transformation could be performed, then the range distribution of reflections in the environment, as characterized by their reflective abilities, could be known.

However, equation (4) is one dimensional, indicating only the range distribution of delays and does not indicate direction. The idea of directional arrays for receiving or transmitting may be added to the characterization to produce equation (5).

$$R(t, A_1, A_2) = \int_0^{\infty} a(\tau, A_1, A_2) P(t - \tau) d\tau \quad (5)$$

A_1 = azimuth angle

A_2 = elevation angle.

In general, the magnitude of a particular value of $R(t - \tau)$ may be maximized by scanning the directional characteristics of an array, mechanically or by phasing, and the sequence of values at that angle and range, for which $R(t - \tau)$ is a maximum, is used to estimate the nature of the reflector by the disposition and magnitude of the reflections.

Thus far, no specific statement of the nature of the stimulus, or transmitted signal, has been entered into the expressions. If we choose the pulse of a single frequency sine wave as that stimulus, the indication of the effect of motion may be entered into equation (5) by equation (6).

$$R(t, w) = \int_0^{\infty} a(\tau) \sin \left[w \left(1 - \frac{v(\tau)}{c} \right) (t - \tau) \right] d\tau \quad (6)$$

The transformation is now two dimensional, entering $v(\tau)$ as a new variable modifying w . The additional information is useful, but requires more bandwidth to accept the shift of frequency consequent to motion. An inverse to this transformation would provide range and motion information at a particular range for characterization of the reflection. By inverse is meant a correspondence formed between the received signal and the range and velocity of the reflections.

It becomes evident that the significance of a received sonar signal lies in the formation of a correspondence to the source of the signal from the received sound. This includes the construction of a statement defining the location in range, azimuth, and altitude (or an equivalent coordinate system) of the source of the observed sound or reflection. It also includes, if possible, the construction of a statement of the size, shape and material of the object or feature at a particular location. The utility of sonar, whether man made or animal, resides in the ability

to use it to characterize the environment, or features of importance in the environment, from the perceived sound. And this task requires the construction of a correspondence between features or sets of features of the received sound and the environment and objects in. Dolphins living in muddy water, or under experimental conditions blindfolded, appear to do this very well; thus it is possible.

Before generalizing mathematically, it may be useful to consider the kinds of sounds which animals, known to use sonar, have been observed to make, and perhaps also natural sounds in general. The dolphin has two general classes of sounds. One of the dolphin sounds is a sharp pulse of sound, or a sequence of sharp pulses of sound; the other is a whistle modulated in frequency. The bat produces a whistle modulated in frequency of many cycles duration, and some species are reported also to use sharp pulses. These are special cases of the class of natural sounds, most of which are sharply transient, such as rustles, snaps, or complex noise in character such as wave and wind noise.

The natural sounds have wide frequency bands. They also have time ordered character due to reflection and propagation phenomena, again as wave noise and wind noise in grass or leaves. Since the information capacity of a channel of communication is dependent on the bandwidth, it might be expected that such sounds are capable of supplying much more information to the perceiver than would be obtainable from narrow band pulses of single sine waves.

Let us examine the consequences of introducing complex sounds into our discussion of sonar. In simple terms, we have an information channel of greater capacity so that we may know more about the environment. At the risk of seeming overly philosophical, we may introduce a point of view. In active sonar, the emitted sound may be considered to be a stimulus and the resultant history of sound considered to be the transformation provided by the environment, or the environment may be thought to be a filter to the signal, and has a transfer function. In behavioral terms the emitted signal is a stimulus and the result a response. In mathematical terms we may write the following:

$$H(s) = P(s) T(s) \quad (7)$$

$P(s)$ = the emitted signal

$T(s)$ = the transformation of the environment

$H(s)$ = the perceived resultant sound

Because it is convenient, the notation implies a linear system described in Laplace Transform notation. The equivalent time description is not so neat, but may be written as equation (8).

$$H(t) = \int_0^{\infty} a(\tau) P(t - \tau) d\tau \quad (8)$$

$a(\tau)$ = an attenuation function of

τ = the delay between emission of P and
its arrival at the point giving $a(\tau)$

$P(t)$ = the emitted signal

$H(t)$ = the perceived resultant sound.

It is more satisfactory to deal with equation (7).

If $P(s)$ is known and an operation can be performed on $H(s)$ such that

$$O_1(s) H(s) = P(s) \quad (9)$$

then

$$O_1(s) = T^{-1}(s) \quad (10)$$

$O_1(s)$ = operation on H

$T^{-1}(s)$ = transform inverse to $T(s)$

$$T^{-1}(s) T(s) = 1 \quad (11)$$

Knowing $T^{-1}(s)$, if an operation can be performed such that

$$O_2(s) T^{-1}(s) = 1 \quad (12)$$

then

$$O_2(s) = T(s) \quad (13)$$

It is sufficient to perform $O_1(s)$ to know $T(s)$, since no information is gained from the succeeding operation $O_2(s)$.

If the desired result is to be obtained from such a sequence, $P(s)$ must be spanning in the geometrical, or vector, sense, if $H(s)$ is to characterize the environment and items of importance in it. In simplest terms, $P(s)$ must be sufficiently complicated to provide a datum in $H(s)$ for each significant datum in the environment.

Three unattainable examples of a complete acoustical spanning may be given:

- (1) a frequency swept whistle from 0 to ∞ in frequency;

- (2) a Dirac impulse of zero duration and unit energy;
- (3) white noise of frequency range from 0 to ∞ .

Since these are unattainable, we may restrict our characterization by domain, stating the largest and smallest features which we wish to characterize, and the density of information required, and rewrite those statements for agreeable partitions:

- (1) a frequency swept whistle of duration from f_l to f_u
 f_l = lower limit of frequency
 f_u = upper limit of frequency;
- (2) a sharp pulse of rise time T_1 , decay time T_2 ;
- (3) a noise band of frequency range f_l to f_u .

We find, pleasantly, that nature has anticipated mathematicians.

Having provided a logical basis, we may now continue to examine "more sophisticated" systems which approach nature. If we wish to determine the spatial coordinates of a sound, we may set up an array of listening posts, as was done for artillery sound ranging, and compare the arrival times of a complex sound at the various positions and from this calculate the location of the source. Or we may actively emit a complex sound and receive on an array and perform a similar calculation. Or we may emit an encoded complex sound from an array and find the location of the source from the recoded message.

In order to exhibit openly the developing viewpoint, we need again a statement of philosophy. The stimulus which results in the environmental sound by transformation is now a "communication channel" and the perceived result a "message". Our task is to "decode" and understand the meaning of the message as concerning environment and features. The process may involve construction of the "inverse" to the environmental "transformation" which wrote the message, thus to relate information in the message to information in the environment, and thus to know the environment.

Suppose we examine at once a sophisticated sonar array and a natural system. This is provided by the human external ear, auricle, or pinna. W. B. McLean demonstrated in the summer of 1959 that distortion of this device also distorted the perception of locale of a sound and thus initiated a study of mechanism. The mechanism is most simply viewed as

a time encoding, provided by a three dimensionally assymetrical mechanical structure, familiarly called the "ear". The encoding involves time delay paths introduced into the sound front amounting to 0-80 microseconds for azimuth, 100-300 microseconds for elevation, and apparently a displaced iteration of that encoding for range. When a steep wave front, as shown in Figure 1, arrives at the ear, it is time encoded as shown in Figure 2.

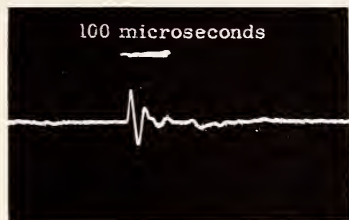


Figure 1. The test pulse.



Figure 2. The test pulse transform by the pinna to the side.

A continuous complex sound is similarly encoded, although not so easily observable, and the characterization thus provided is sufficient both to pay attention to a sound and to localize it. Thus monaural localization is possible, and demonstrable [1].

For sonar systems, such an encoding provides a simple message, and for animals, such an encoding permits three dimensional behavior in an acoustical environment. The ears of dog, cat, mouse, prairie dog, bat, horse, cow, deer, moose, gibbon, and monkey (to mention only those I have examined personally) show the requisite complex sound transforming structure either across the whole pinna or at the base (in cases where the ear is directable). Owl, pigeon, and chicken have pinnae made of feathers which are dense and sound reflecting, covered with acoustically transparent feathers, thus accomplishing the same function (in the case of the owl, very well) [2]. Griffin has reported that the monaural bat also manages to navigate [3].

If we consider a hypothesis of process applicable to the function just described, it is the recognition of the encoding of locale, decided by the transformation needed to pay attention, or select the focus of

attention, used to improve the signal-to-noise ratio for that locale by application of the recognition transformation. In order to test the validity of this hypothesis of process, we constructed computer programs to construct inverses to known inputs by process not making use of our knowledge of the input, assuming a pulse stimulus. The recognition transformation was then subjected to the same process, and the message reconstituted. These are shown in Figure 3 and Figure 4. The decision of recognition is based solely on the recovery of the stimulus.

The theory applicable again requires a philosophical statement. (Somewhat apologetically, I must affirm that my activities have a philosophical base.) The statements applicable here are as follows:

1. One cannot be informed of what one knows.
2. Removing the message from the channel by a knowing process leaves only the stimulus.

We thus search for processes which systematically produce the inverse transformation, thus destroying the message and leaving only the empty channel (or stimulus and space).

If we continue now to examine our recognition process, we see that it may be applicable not only to localization, but also to environment and object recognition. The pulse emitted by a dolphin is transformed by the head structure through which it emerges into the water. The resultant complex encoding is again transformed by the environment and objects. If the initial character is known, it may be used to improve the signal-to-noise ratio of the second message. After which, the same process of recognition details the environment or its selected features. Characterization by locale may also be used to enhance the message from a particular point, and adaptation of the initial encoding to maximize particular object selection is possible. In vector or geometrical terms, the partition is constructed to accept the transformation of interest.

From a different viewpoint, this is a well established study [4]. We have attempted to include features not considered in these earlier programs. Because of the importance to natural sounds as contrasted to man contrived sonar, we must examine some characteristics of the

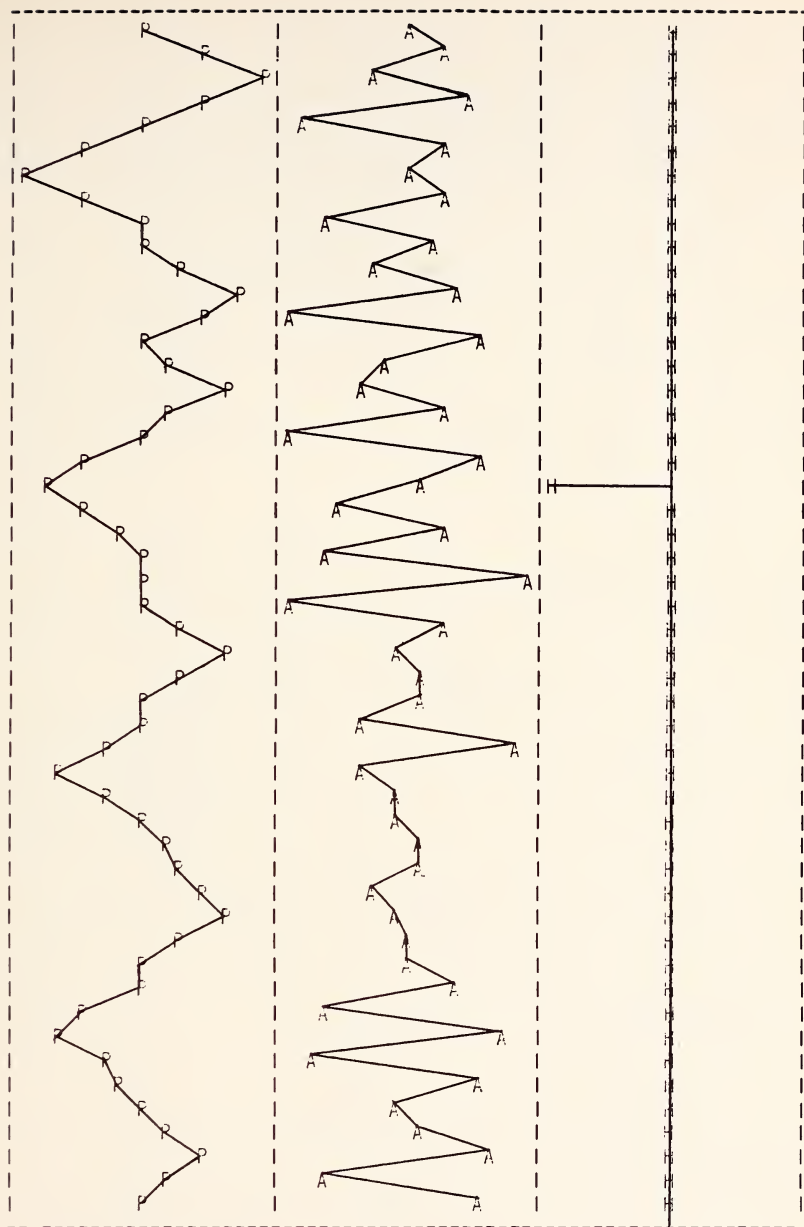


Figure 3. Result of computation on the synthetic input $H(x)$, giving the attention function $A(x)$, decided by the spike in the output, $D(x)$.

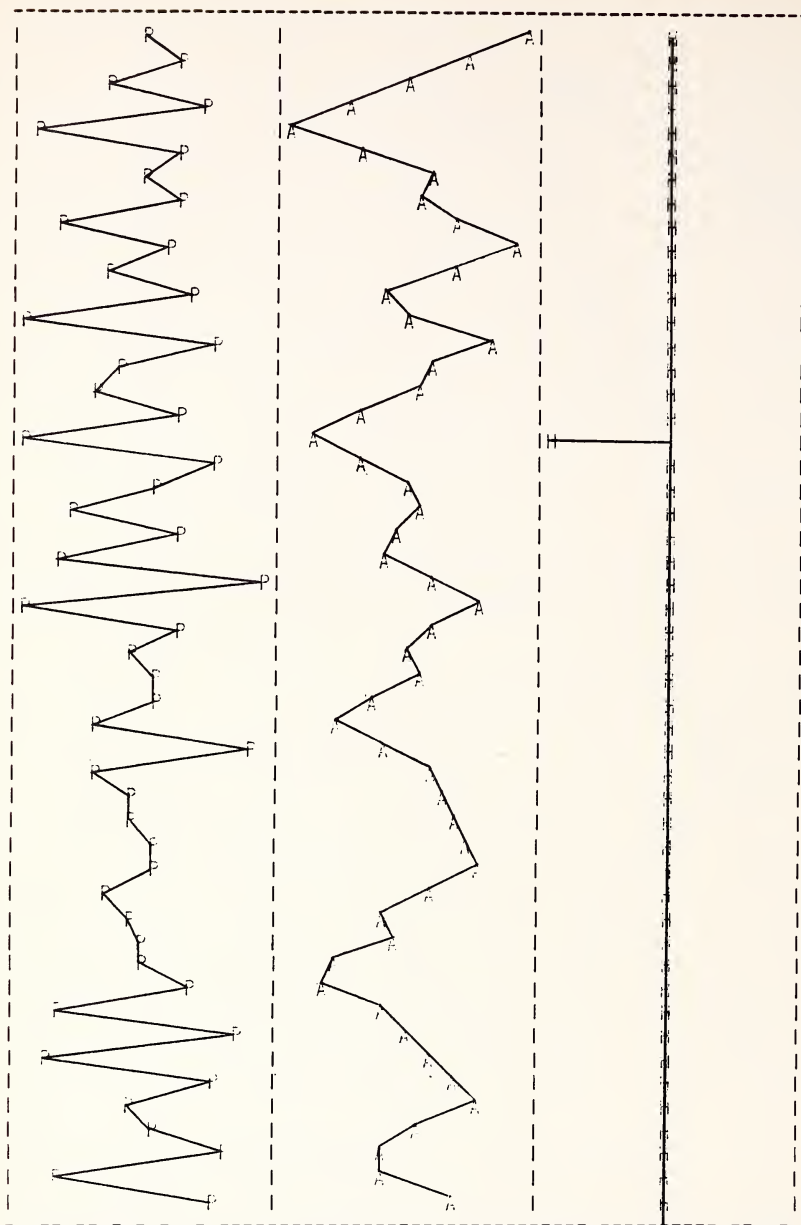
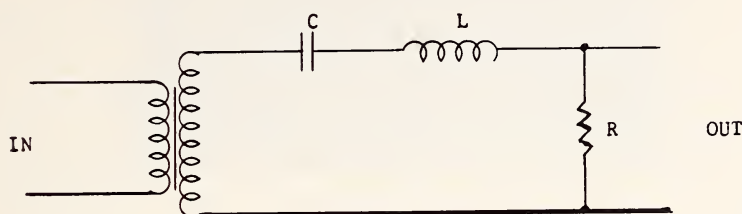


Figure 4. Verification of $A(x)$ as $T^{-1}(x)$ where $H(x) = D(x) T(x)$ by recovery of $A(x)$ by process giving $D(x)$.

transformations concerned. In network theory we can look at two classes of networks with distinct properties; these are planar and non-planar (there are, of course, others). The planar network is one which can be drawn in a plane without crossing lines as shown in Figure 5. The non-planar network cannot be so drawn, but requires two planes, or a three dimensional space for its realization, as shown in Figure 6.



$$\frac{e_o}{e_i} = a \frac{R}{R + j(x_1 - x_c)}$$

Figure 5. Planar network, amplitude and phase dependent.

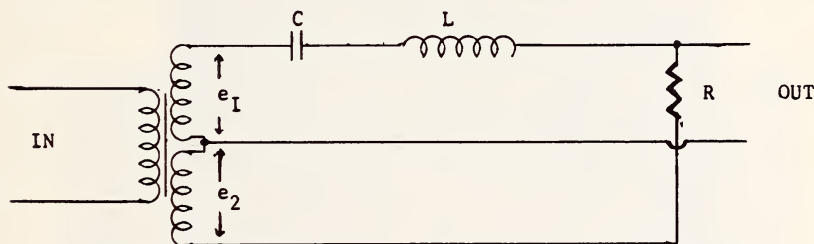


Figure 6. Non-planar network, amplitude and phase independent.

$$\frac{e_o}{e_i} = a \left[\frac{R}{R + j(x_1 - x_c)} - b \right] ; e_1 a b = e_2$$

If b in Figure 6 is given a special value

$$b = \frac{1}{2}$$

then

$$\frac{e_o}{e_i} = \left(\frac{-a}{2} \right) \left[\frac{R - j(X_1 - X_c)}{R + j(X_1 - X_c)} \right]$$

$$\text{Mod } \frac{e_0}{e_1} = \frac{a}{2} \text{ a real constant}$$

$$\text{Arg } \frac{e_0}{e_1} = 2 \arctan \frac{X_c - X_1}{R}$$

The planar network has a functional dependence between phase and frequency functions, so that either is equally informative. In this case information can be carried by frequency power density distribution functions alone. The result can be characterized by conventional spectrum analysis of signals and the autocorrelation function carries the same information. However, the non-planar networks do not have a functional relationship between phase and frequency functions and both phase and amplitude are informative. This means that there are transformations whose frequency power density distribution does not characterize the transformation or does not carry the whole message, as illustrated by Figure 7 and Figure 8.

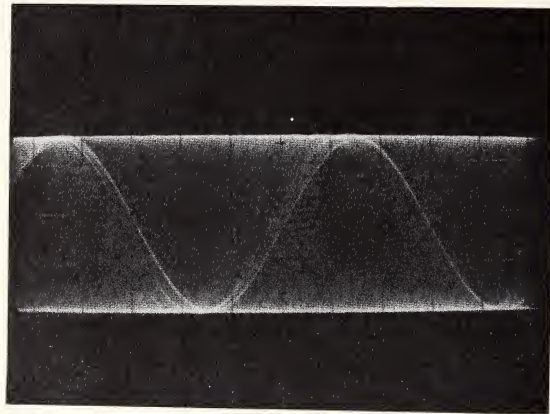


Figure 7. Swept oscillator direct output.

Natural circumstances are non-planar, and only in particularly contrived and limited man made domains are frequency functions carriers of messages. The extreme example of the difference is given by white noise and a Dirac impulse, each of which has the same autocorrelation function and frequency power density distribution. We thus require that increasing sophistication in Sonar systems again approach nature and use both phase and frequency as informative. It also means that autocorrelation functions and all equivalent analyses are inadequate descriptions of natural sounds.

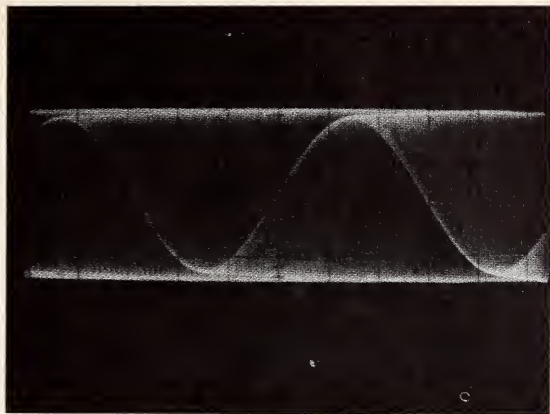


Figure 8. Output of non-planar filter
with swept oscillator input.

The shape of a natural sound is informative. That shape may be distorted without altering its autocorrelation function, as shown by Figure 9 and Figure 10.

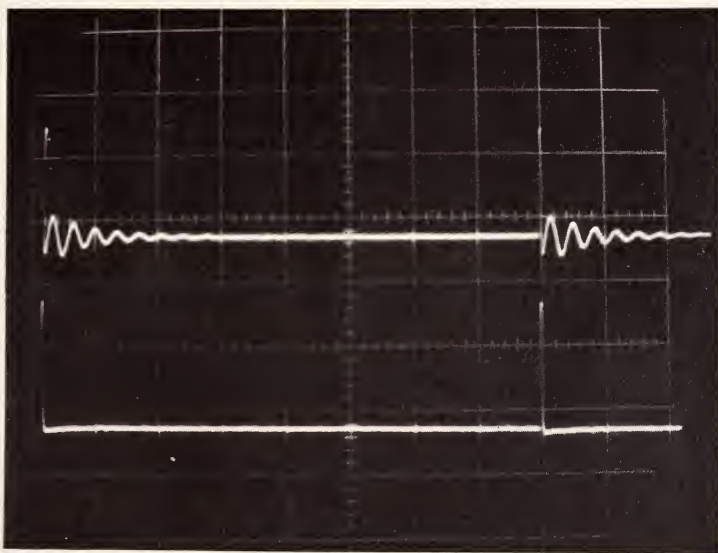


Figure 9. Both signals have the same
autocorrelation function
and spectrum.

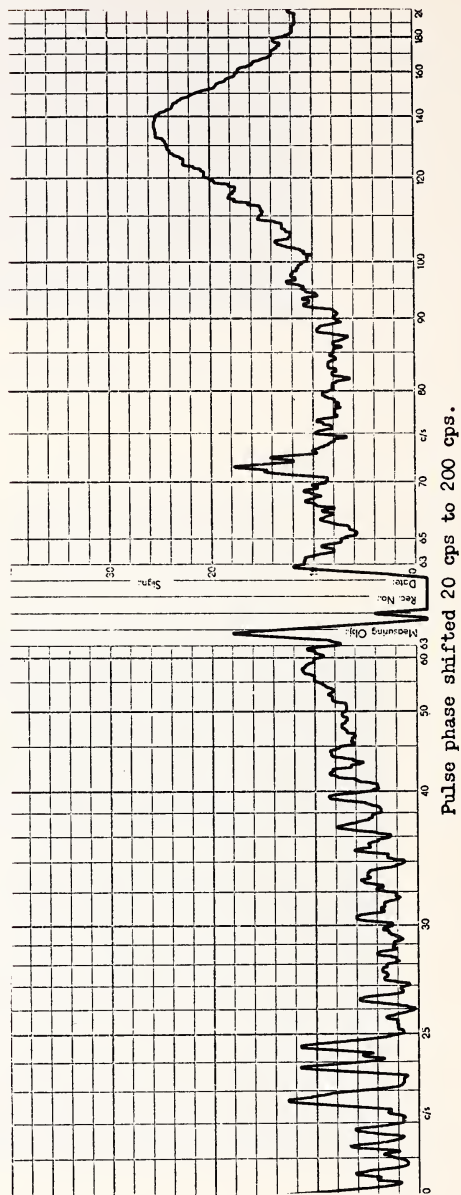
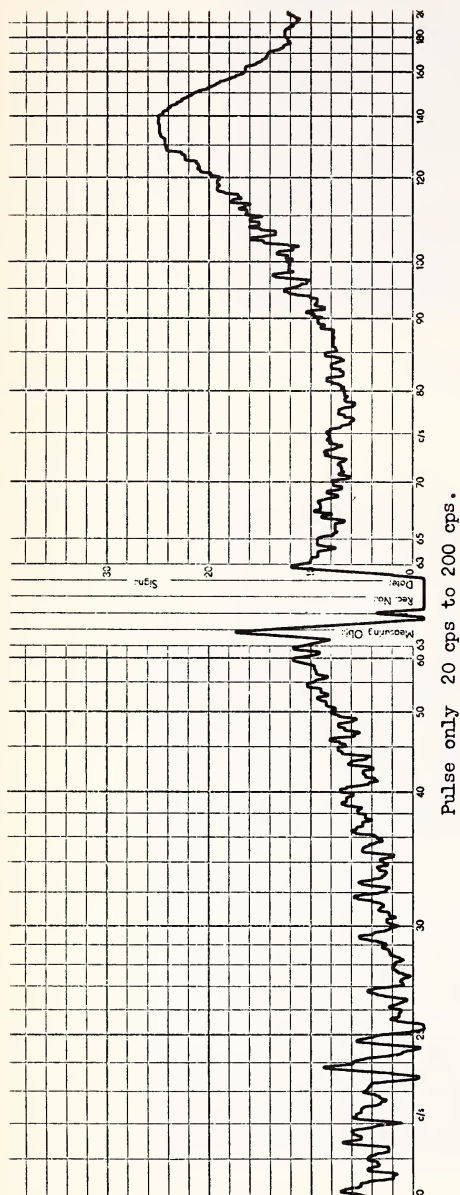


Figure 10. Spectrum analysis of signals from Figure 9.

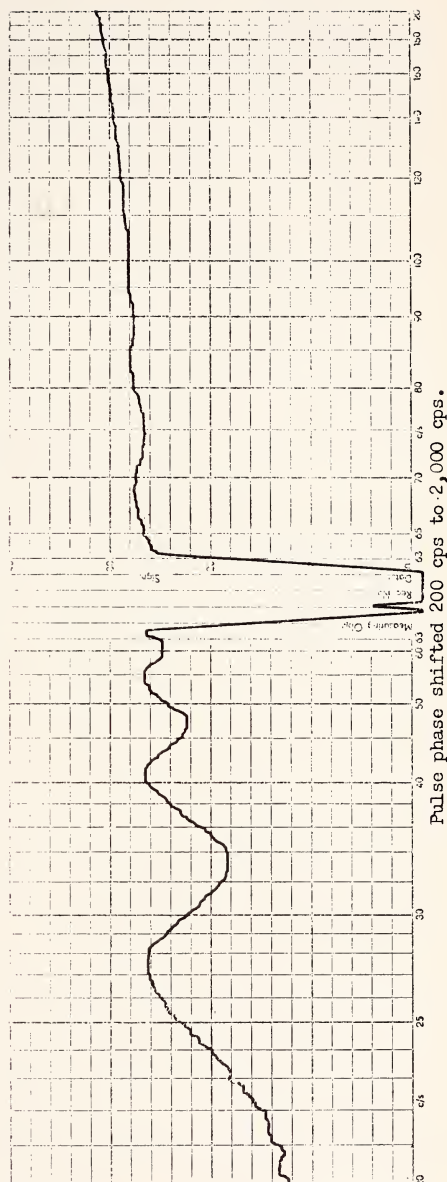
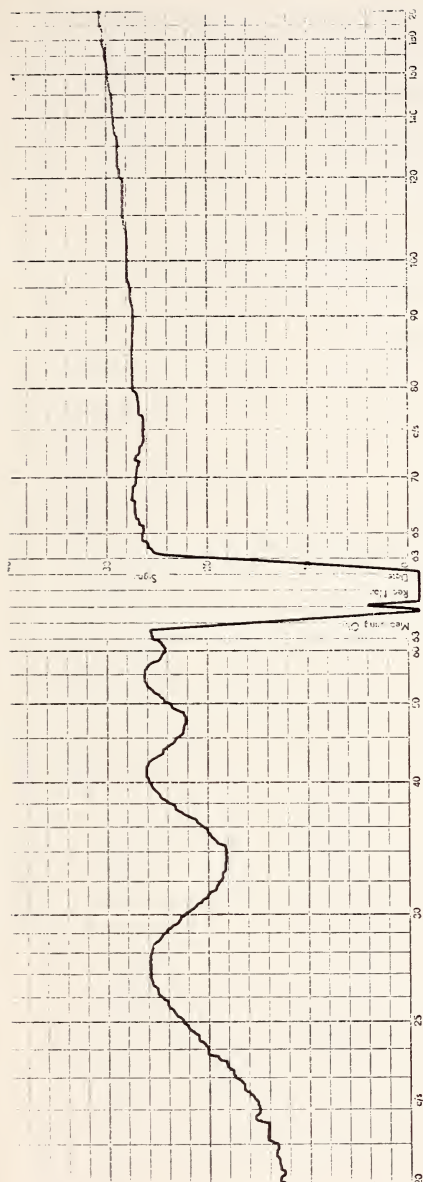
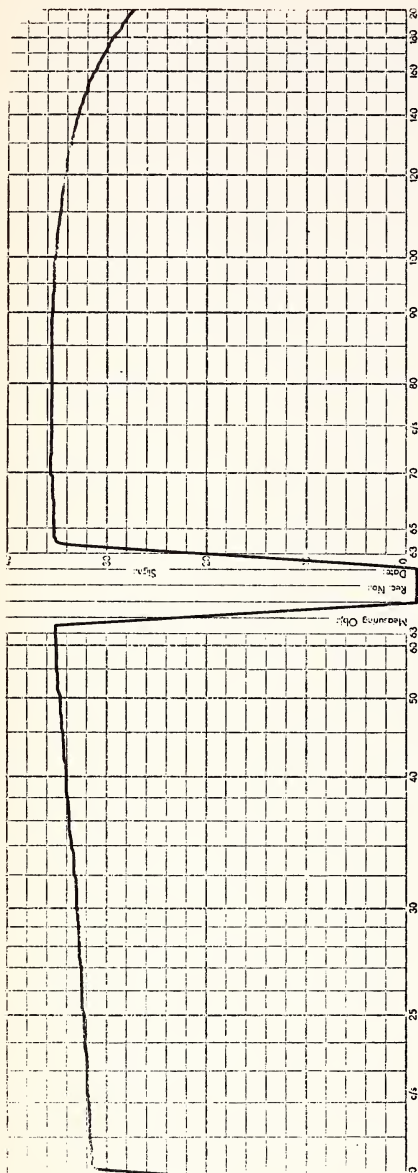
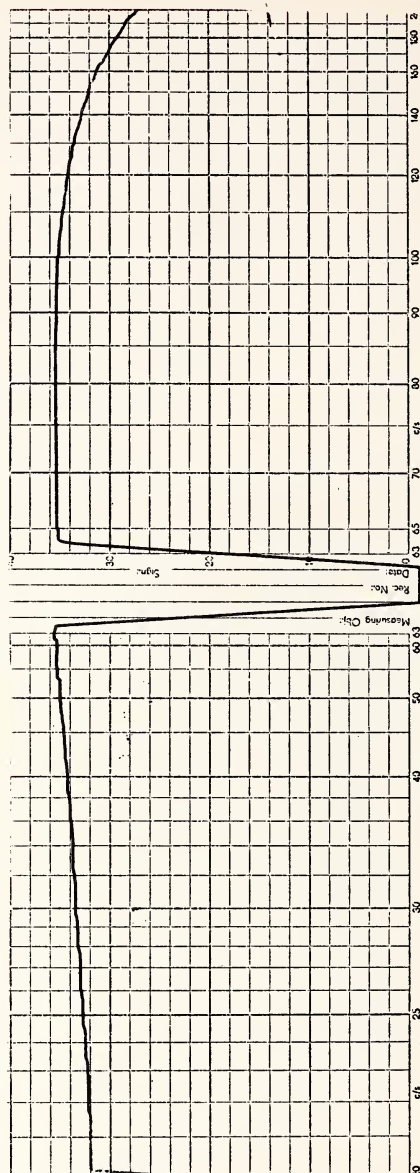


Figure 10. Spectrum analysis of signals from Figure 9.



Pulse only 2,000 cps to 20,000 cps.



Pulse phase shifted 2,000 cps to 20,000 cps.

Figure 10. Spectrum analysis of signals from Figure 9.

In applying our theories of sonar to natural sounds, we must then be careful to be complete. This will permit us to design more effective sonar systems and to understand more completely the character and significance of natural sounds. The use of the characterizing transformation and its inverse necessarily preserves all information, and thus offers the most promising approach to the study of natural sounds and to the design of sonar systems.

If we return to the consideration of the first class of sounds, swept sine waves, the description of equation (a) becomes a limit where a single frequency is used. The result of a single frequency used to illuminate an environment acoustically is an interference pattern, as indicated in Figure 11. It may be assumed that the space and time distribution of the pattern is characteristic of the transformation, and conjecture that measurements could be made which would permit the construction of an inverse. This would require four independent measurements in space and time for each reflecting feature in the environment. However, if the features of the environment are in motion relative to the sonic illumination, then the interference pattern moves around as indicated for simple rotation in Figure 12. A stationary observer using an array of receivers might gather sufficient information to know the environment. However, if there are significant reflectors which are stationary, these would be ignored. One way to move the interference pattern, other than reflector motion, is to sweep the illuminating frequencies, producing motion of the regions of reinforcement and cancellation of the waves. A receiving array would perceive the changes, which would be informative regarding the locations of the reflections.

Another source of information from this kind of illumination is now currently called sound coloration. Since no material reflects all frequencies equally well, if the energy in the unaltered illumination is equally distributed across the frequencies, the result sonically compares to the coloration introduced into white light upon reflection from green leaves, brown twigs, and red birds. Experiments have been conducted in air showing the coloration effects of sound by various materials. [5]

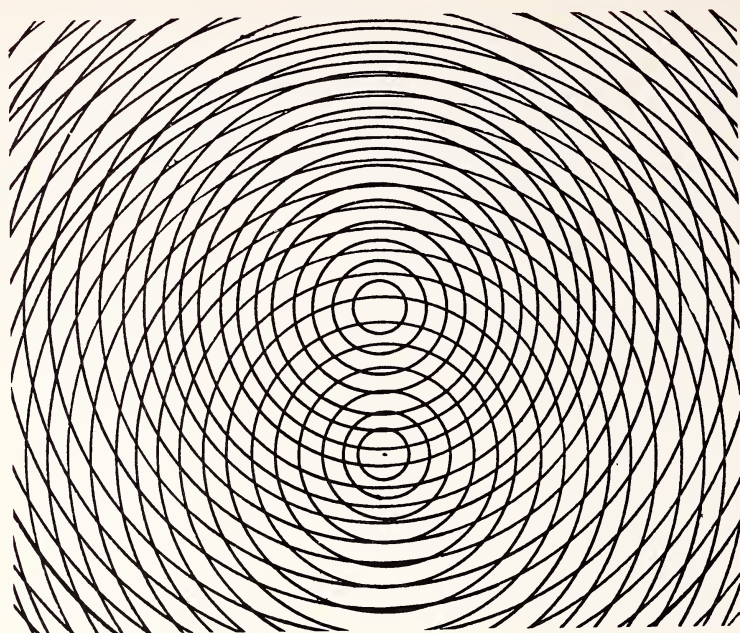


Figure 11. Stationary interference.

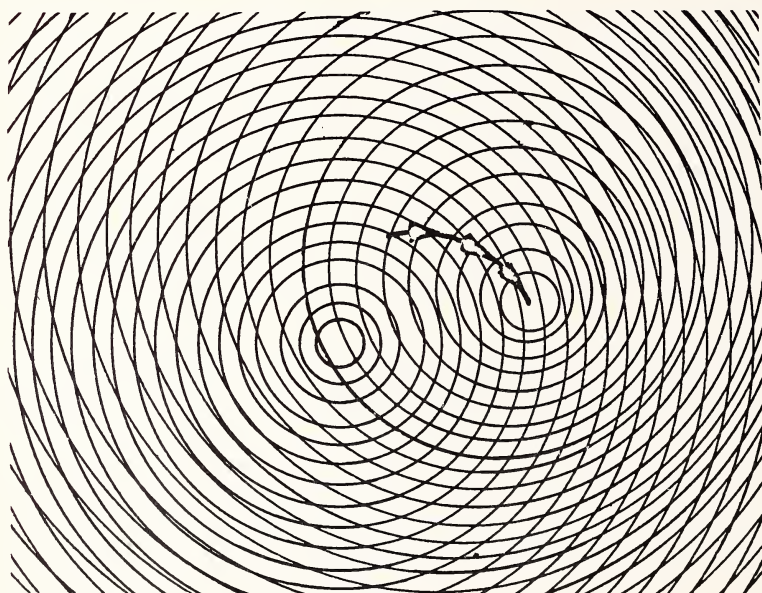


Figure 12. Moving interference.

When we examine the third class of illumination, noise, we find that the interference patterns are not well established as in the case of the sine wave illumination, since phases in noise are random. However, the coloration of noise is easy to observe, and sighs and hisses are examples. The sigh being typically red and the hiss being typically blue.

When white noise is used to illuminate an environment, phase information in the components is minimized, but the amplitude differences are maximized. In this case stone walls, grass, rocks and animals respond with a characteristic coloration of the sound and may be classified accordingly.

When we examine the second class of sounds, we have coherence in phase and broad spectrum so that both coloration and time relationships are preserved. Where a system of reflection produces a moving interference pattern to swept sine waves, and an incoherent pattern-to-noise, the pulses are patterned and moving in time and colored by the characteristics of the reflections. It seems possible that such a system is the most informative, and studies have shown that time encoded messages, or pulse position coding is efficient.

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DISCUSSION

by
D. CAHLANDER

INTRODUCTION

Bats and other animals that use active sonar have several problems. Assume for the moment that you are a bat flying around trying to catch an insect. First you must be able to "know where you are", to navigate. Second you must be able to detect a target that is in the near vicinity. Now, assuming that you know there is a target nearby, you must attack the target, and catch it, assuming of course that it is an edible target. To catch the target you must know what is the distance from the target, what is its azimuth and what is its elevation. To decide whether it is an edible target you must determine something about the size and the shape of the target. All these things a bat must do to catch a supper.

IDEAL RECEIVER MODEL

If a suitable (and simple) model is made of the sonar system of the bat, one can ask what is the best that an "ideal receiver" can do with the bat's signals. Some of the interesting characteristics of ideal receivers that have been developed in the radar literature apply to bats.

The model chosen consists of a moving target at some distance from the receiver, as shown in Figure 1.

The signal at the receiver input is:

$$\text{Eq. 1} \quad y(t) = \sqrt{a} s [a(t-\tau)] + n(t)$$

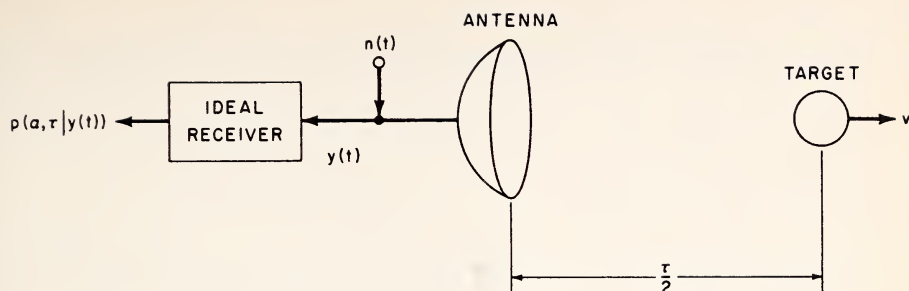


Figure 1. Model of Echolocation System for Determination of Time Delay and Doppler Shift

where

$y(t)$ = received signal

$s(t)$ = transmitted or expected signal

$n(t)$ = additive Gaussian noise

τ = time delay associated with the range of the target

$$a = \left[\frac{1 - \frac{v}{c}}{1 + \frac{v}{c}} \right] = \text{Doppler factor}$$

v = target velocity or range rate

c = speed of propagation

The $\sqrt{a}$ term multiplying the signal in equation (1) makes the signal term have an energy independent of the velocity of the target. This is, in effect, an assumption that the target cross-section is independent of the velocity of the target.

The definition of an ideal receiver is a system that destroys all unwanted information in a received signal and retains all wanted information. In the system described, the desired information is the range ($c\tau/2$) and the Doppler factor (a) of the target; all other information is unwanted. Since the additive Gaussian

noise is statistical in nature the output of the ideal receiver is also of a statistical nature. All the information contained in $y(t)$ concerning τ and α can be expressed as the joint conditional probability density function for τ and α given $y(t)$:

$$\text{Eq. 2} \quad p(\tau, \alpha | y(t))$$

No additional processing of the received signal can extract more information concerning the values of τ and α . Also, in obtaining this probability function, there has been no information about τ and α that has been destroyed. Therefore, a receiver that computes $p(\tau, \alpha | y(t))$, or something monotonically related to this, is the ideal receiver for this problem.

It can be shown that:

$$\text{Eq. 3} \quad p(\tau, \alpha | y(t)) = k p(\tau, \alpha) \exp \left[-\frac{E}{N_0} \right] \exp \left[\frac{2 \sqrt{E \alpha}}{N_0} \int y(t) u[\alpha(t-\tau)] dt \right]$$

where

$$E = \int s^2(t) dt$$

the energy of the received signal

$$u(t) = \frac{1}{\sqrt{E}} s(t)$$

the normalized received signal

$$N_0 =$$

noise energy/Hz

$$p(\tau, \alpha) =$$

the a priori probability density function for τ and α

The operation of the receiver on the received signal is contained in the exponent of the last factor:

$$\text{Eq. 4} \quad q(\tau, \alpha) = \frac{2 \sqrt{E \alpha}}{N_0} \int y(t) u[\alpha(t-\tau)] dt$$

But $y(t)$ is the sum of two terms, the signal term and the noise term. Assuming the target was actually at τ_0 with a Doppler factor α_0

$$\text{Eq. 5} \quad q(\tau, \alpha) = h(\tau, \alpha) + g(\tau, \alpha)$$

$$\text{Eq. 6} \quad h(\tau, \alpha) = \frac{2 \sqrt{E \alpha}}{N_0} \int n(t) u[\alpha(t-\tau)] dt$$

$$\text{Eq. 7} \quad g(\tau, \alpha) = \frac{2 E \sqrt{\alpha \alpha_0}}{N_0} \int u[\alpha_0(t-\tau_0)] u[\alpha(t-\tau)] dt$$

It can be shown that since $n(t)$ is white Gaussian noise, $h(\tau, \alpha)$ is a Gaussian variable where

$$\text{mean} = 0$$

$$\text{variance} = \frac{2E}{N_0} \equiv R$$

The signal function is derived from the $g(\tau, \alpha)$ term, by allowing $\alpha_0 = 1$ and $\tau_0 = 0$ and removing the energy term $\frac{2E}{N_0}$

$$\text{Eq. 8} \quad \chi(\tau, \alpha) = \int u(t) u[a(t - \tau)] \sqrt{\alpha} \, dt$$

or alternately:

$$\text{Eq. 9} \quad \chi(\tau, \alpha) = \int U^*(\alpha\omega) U(\omega) e^{-j\alpha\omega\tau} \sqrt{\alpha} \frac{d\omega}{2\pi}$$

There are several conditions which limit the type of function that $\chi(\tau, \alpha)$ can be. Since this function characterizes the range and range rate resolution limitations of an echolocation system, it is interesting to look at some of its properties.

$\chi(\tau, \alpha)$ is a cross-correlation between two signals of unit energy; therefore

$$\text{Eq. 10} \quad \chi(0, 1) = 1 \geq \chi(\tau, \alpha)$$

The height of the signal function is related monotonically to the likelihood that the target is at some particular range traveling at some particular velocity.

Over the region that the signal function has a value close to one, the values of range and range rate are indistinguishable or ambiguous. Therefore, the most desirable echolocation signal would be one for which the signal function takes on a value of one at (0,1), and zero or a negative value elsewhere. It can be shown however that

$$\text{Eq. 11} \quad \int_{-\infty}^{\infty} \int_0^{\infty} |\chi(\tau, \alpha)|^2 \frac{\omega_0 d\alpha}{2\pi} d\tau = \frac{1}{2} \left[1 + \left(\frac{\beta}{2\omega_0} \right)^2 - \dots \right]$$

where ω_0 = the mean frequency of the transmitted signal
 β = the band width of this signal

This is an important result. This states roughly that the volume under the signal function is a constant. Different transmitted signals just change the position of the fixed volume contained by the signal function, not unlike moving around a fixed amount of sand in a box.

ANALYSIS OF BAT SONAR SIGNALS

Signals of two species of vespertilionid bats, Myotis lucifugus and Lasiurus borealis, were picked up by a microphone and recorded while the bats were in the pursuit of thrown targets. The signals of the Myotis were obtained in the laboratory of Frederic A. Webster; the signals of the Lasiurus were obtained in the field.

Since the microphone that was used was not perfect, the microphone changed the nature of the bat signal slightly. Off the main axis of the microphone, the microphone had zeros in its frequency response. The general response of the microphone is given roughly by:

$$\text{Eq. 12} \quad s(\omega) = \frac{2J_1(a\omega \sin \theta)}{a\omega \sin \theta}$$

where $J_1(x)$ is the first order Bessel function. Since the position of the bat during pursuit of the target was known, the microphone was aimed in such a way that the bat flew on the axis of the microphone most of the time. This was not too difficult, since the beam width of the microphone at the highest frequency that the bat used was on the order of 30° .

MYOTIS LUCIFUGUS

The bat Myotis lucifugus is the little brown bat common to the New England area. The full grown adult has a maximum wing spread of about 10 inches, and weighs between 5 and 12 grams. The bat's diet consists largely of insects that are caught in flight. It has some eyesight but this is barely more than a discrimination between light and no light. If the bat is placed in a dish containing food, too

close for it to make use of its sonar, it moves in a random fashion until its nose actually bumps into some of the food before it realizes where it is in the dish.

The Myotis was trained to catch mealworms that were shot into its path by a "mealworm mortar". It would circle the room passing over the mortar until a mealworm was shot to it. One or two microphones, placed in the path of its flight, obtained tape recordings of its sonar signals while it was in pursuit of a target. Figure 2 illustrates the wide variation in the type of signal used in pursuit of its target. It is an oscillographic record made from tape recordings. The upper trace is the sound pressure on one microphone; the lower trace is the sound pressure on a second microphone, simultaneously recorded. The distortions of the amplitude waveform are partially due to the gain pattern of the bat's emitted signal, the gain pattern of the microphones, and the inclusion of additive multipath echoes. The position of the bat can be determined relative to the positions of the two microphones by measuring the relative time delay between a particular pulse on the two signal tracks.

Five representative pulses were chosen from this sequence, on the basis of being "typical" and having a high signal-to-noise ratio. These pulses, assigned the numbers 2, 3, 4, 5, and 6, as indicated in Figure 2, were analyzed in detail by means of an ambiguity diagram computer. This computer plots $\chi(\tau, \alpha)$ for each signal pulse.

The first signal to be analyzed is designated as "pulse 2" in Figure 2. Figure 3 shows a more detailed photograph of the pulse along with a plot of the instantaneous period of the pulse. This "instantaneous period" is the time between positive-going zero-crossings of the sound pressure waveform. It can be considered the inverse of the instantaneous frequency of the signal. The snow effect that is seen in this display when a pulse is not present is due to the period

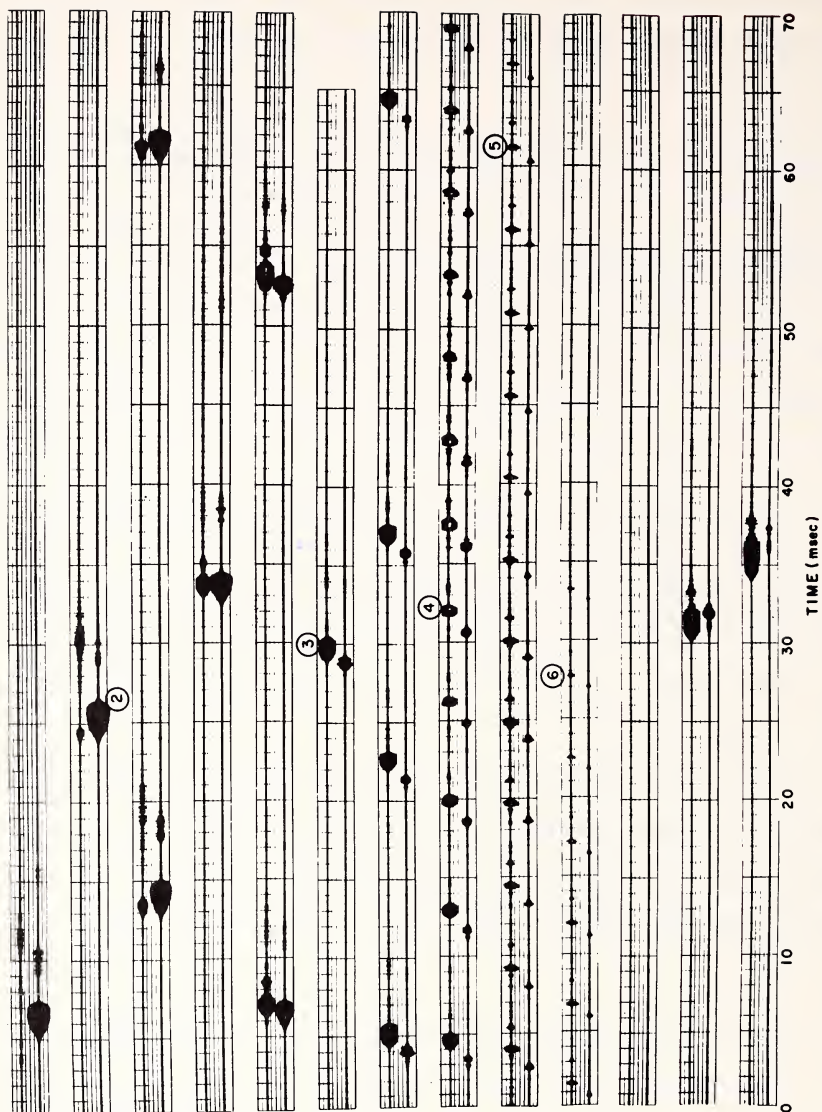


Figure 2. The sounds emitted by a *Myotis lucifugus* while cruising, then in pursuit of a target, as picked up by two microphones and recorded on a continuous oscillographic record. The vertical lines are time markers, spaced 1 msec apart. The length of each strip is 70 msec, except the one which was cut short to avoid splitting a pulse.

meter being triggered by noise with random zero-crossings.

Pulse 2 is almost sinusoidal with a period that is steadily increasing in a slightly non-linear fashion. This pulse is designated as a cruising pulse. The bat uses a pulse like this when it is cruising in search of food, but has not yet located any targets. The starting frequency of this pulse is 100 kc; the final frequency is 40 kc; the duration is 3.2 msec.

Figure 4 shows a three-dimensional drawing of the ambiguity diagram for this pulse. The width of the area of ambiguity, if the velocity of the target is known to be zero, is about $85 \mu\text{sec}$. One of the interesting things about this ambiguity diagram is that the fine structure of the ambiguity surface is on approximately the same scale as the coarse structure. If the signal-to-noise ratio were high enough, and the velocity of the target were known, the measurement accuracy of the target range would be limited only by the width in the time-delay direction, of the central spike of this surface. If the same modulation were used on a much higher frequency carrier, the area of ambiguity would be determined by roughly the upper

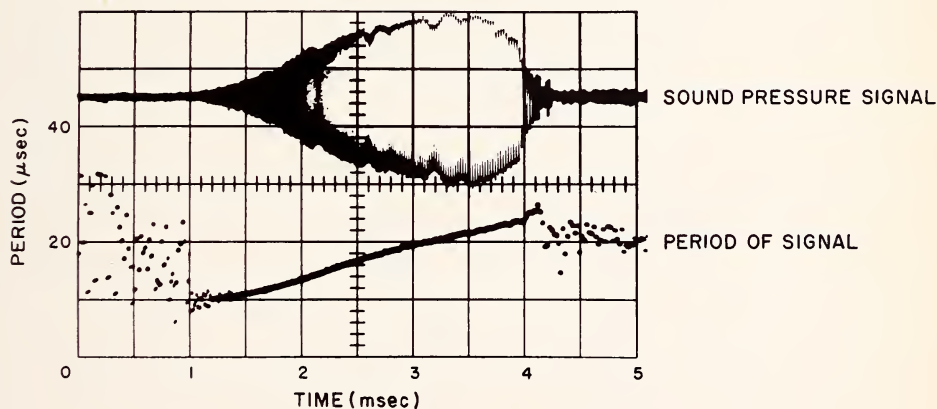


Figure 3. Myotis Lucifugus Cruising Pulse (Pulse No.2)

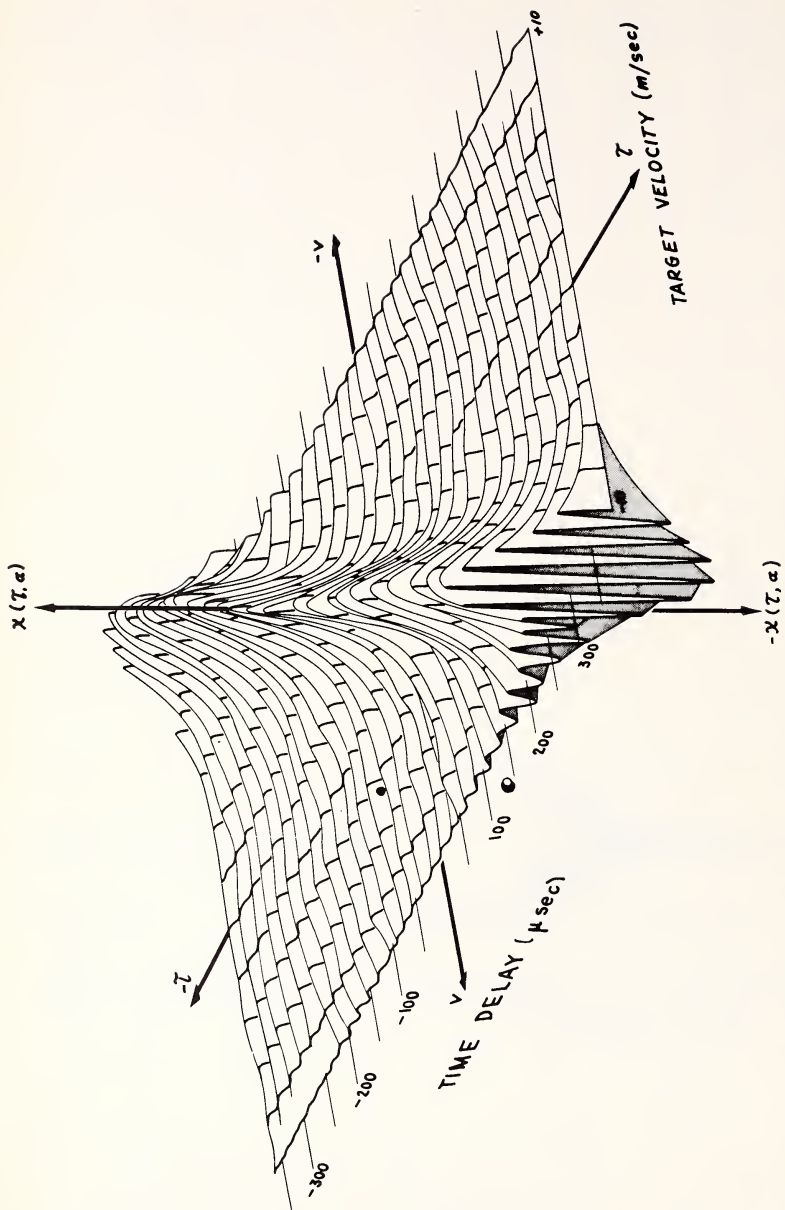


Figure 4. Cruising-Pulse Ambiguity Diagram For Myotis Lucifugus (Pulse No. 2)

envelope of this surface of ambiguity. The upper envelope of this surface can be visualized as the surface that would result if a silk scarf were laid over the entire surface. The ratio of the width of the envelope to the width of the central spike for this particular ambiguity diagram is approximately 7:1.

Figure 5 shows the second signal that is analyzed (designated "pulse 3").

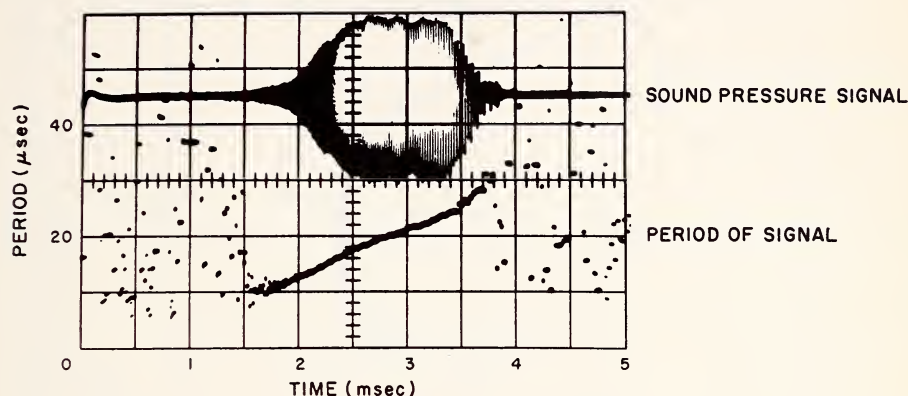


Figure 5. Myotis Lucifugus Locating Pulse (Pulse No.3)

Figure 2 displays the position of this signal in the over-all pulse train. This pulse occurs either just before or just after the bat detects the target. Detection of the target is followed by the decrease in the inter-pulse period that can be seen graphically in Figure 2 and is plotted in Figure 6. The inter-pulse period varies during cruising between 20 and 100 msec. When the bat detects the target, the inter-pulse period drops, the duration of the bat's signal decreases, and the rate of change of frequency increases. In this particular plot, the inter-pulse period is relatively constant and then decreases sharply. The constant inter-pulse period before detection of the target is not typical of the general case. Usually the inter-pulse period varies up and down in a rather random fashion until the bat detects the target; the inter-pulse period then decreases as shown in Figure 6. The jump in the inter-pulse period just before the long sequence of closely spaced pulses is present in many cases. It has been hypothesized that this is due to the

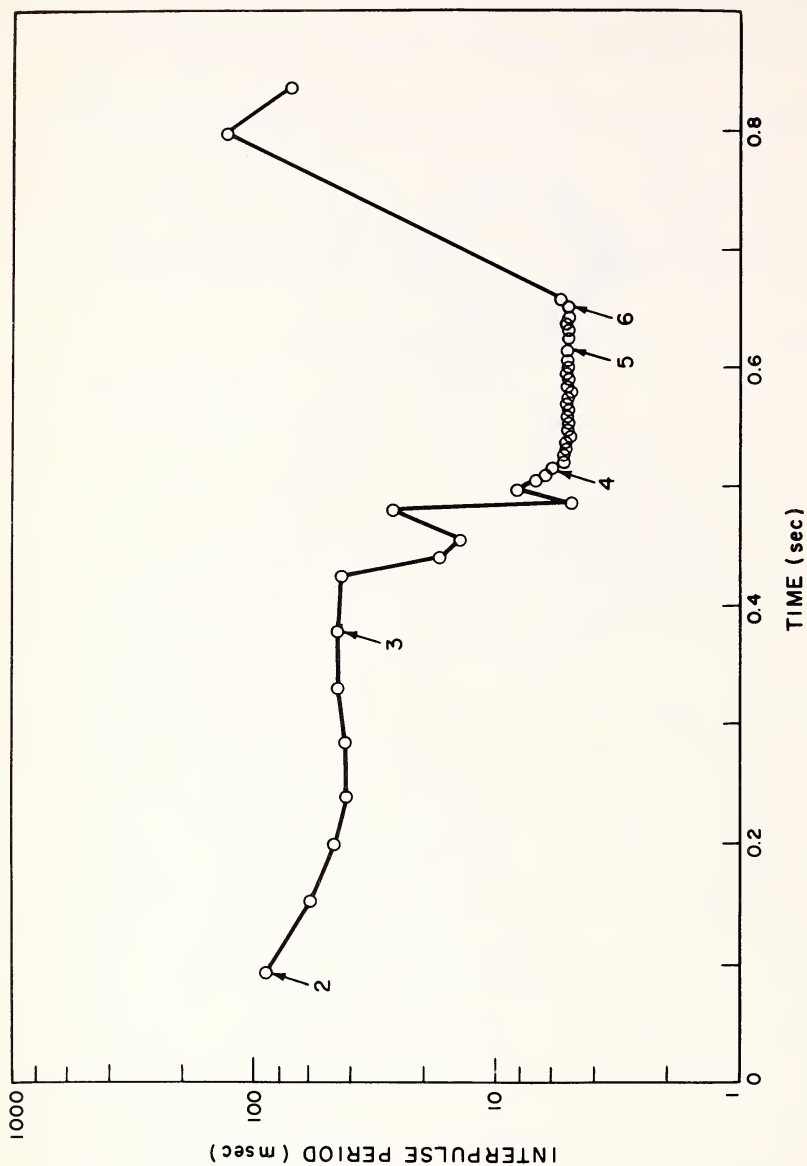


Figure 6. Time interval between a pulse and the preceding pulse for the record shown in Figure 2. The small numbers inside the circles correspond to the numbers assigned to the individual pulses.

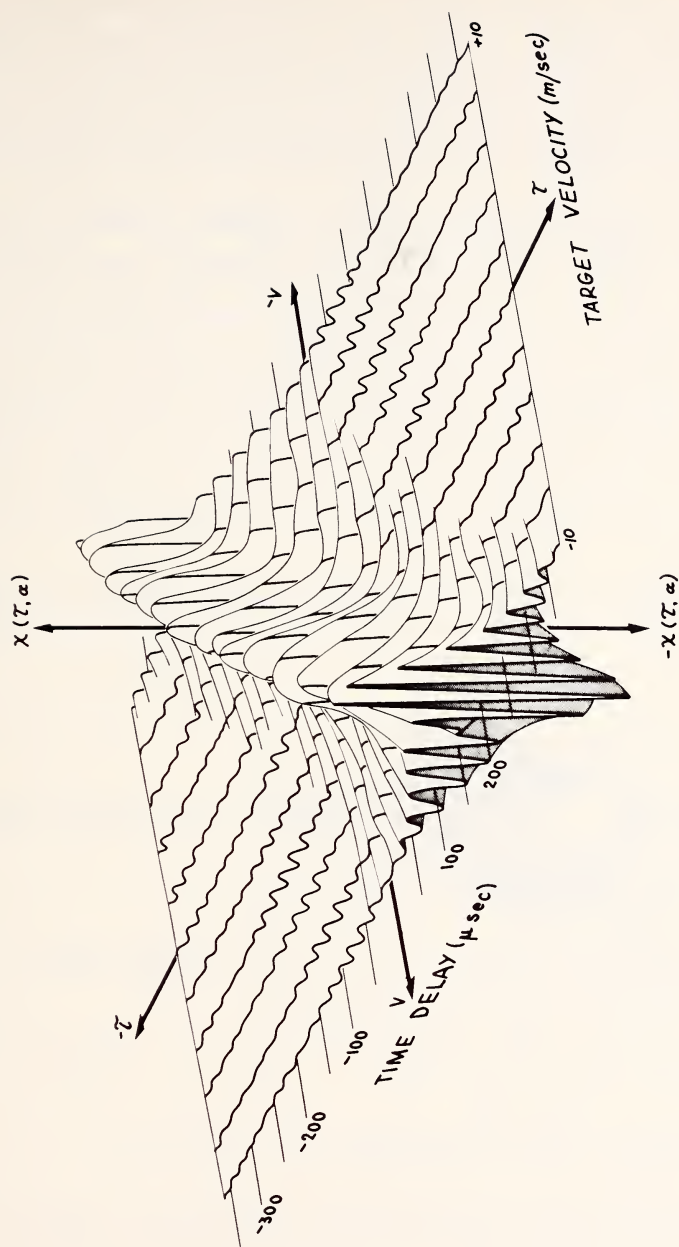


Figure 7. Locating-Pulse Ambiguity Diagram for Myotis Lucifugus (Pulse No.3)

bat taking in a breath of air so that he can emit the entire sequence of closely spaced pulses with one breath. In this case, the relatively constant amount of inter-pulse period before detection might be due to the fact that the bat knew that a mealworm was being thrown and was searching a known area for the target.

Figure 7 shows a three-dimensional drawing of the ambiguity diagram for pulse no. 3. The over-all nature of this surface is very similar to the ambiguity diagram for pulse no. 2. This is interesting since the shape, the duration and the frequency modulation of pulse no. 3 are somewhat different from those of pulse no. 2. A close examination of the structure of the ambiguity diagram for pulse no. 3 reveals that the parameters of this surface are different. The width of the $v = 0$ slice of the surface is $70 \mu\text{sec}$ and the width of the $v = 10$ slice is $100 \mu\text{sec}$.

Pulse 4 is emitted after the bat has located the target. Figure 8 is a photograph of pulse 4.

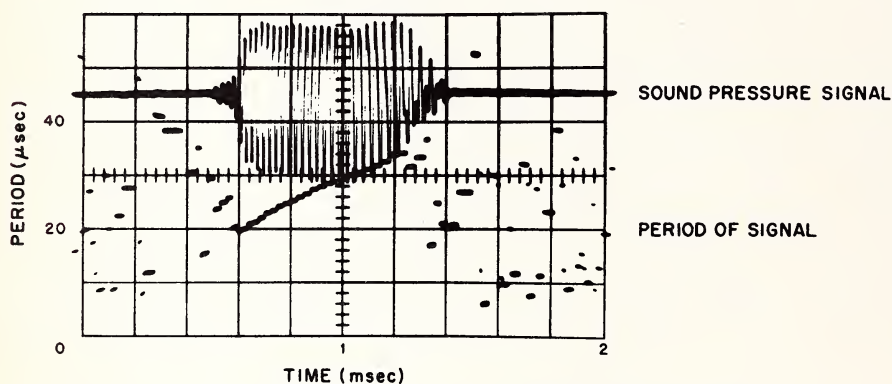


Figure 8. Myotis Lucifugus Pursuit Pulse (Pulse No.4).

The upper frequency of pulse 4 is about one-half what it was for pulses 2 and 3, and the duration has decreased in pulse 4. Figure 9 illustrates a three-dimensional

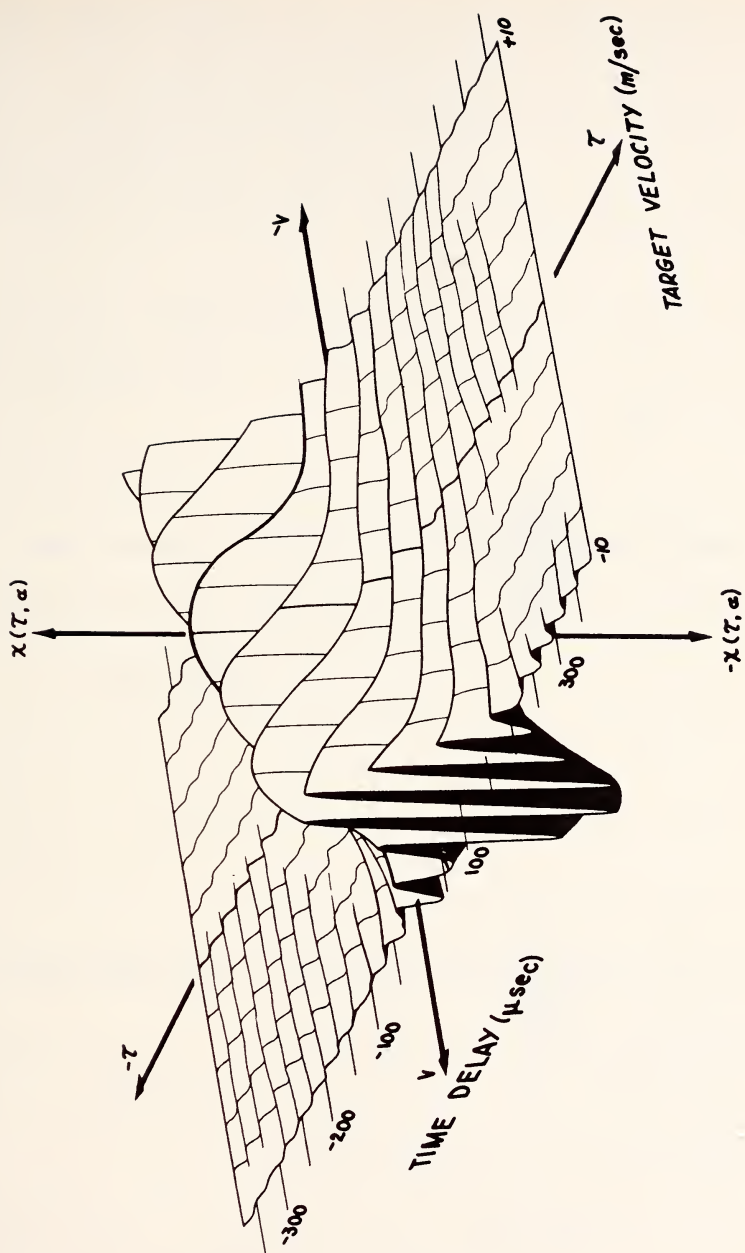


Figure 9. Pursuit-pulse Ambiguity Diagram for Myotis Lucifugus (Pulse No.4)

drawing of the ambiguity diagram for pulse no. 4. This ambiguity diagram illustrates the general trend that, as the bat approaches the target, he uses a pulse that gives him a smaller amount of range error for a given velocity error. While the ambiguity diagram for pulse 2 has nearly 30 maxima (for the amount of diagram illustrated) and the ambiguity diagram for pulse 3 has 15 maxima, the ambiguity diagram for pulse 4 has only 7 maxima.

The bat emits pulses 5 and 6 when it is very close to the target. It knows where the target is and inspects it to determine if it changes course. Figures 10 and 11 illustrate these two pulses.

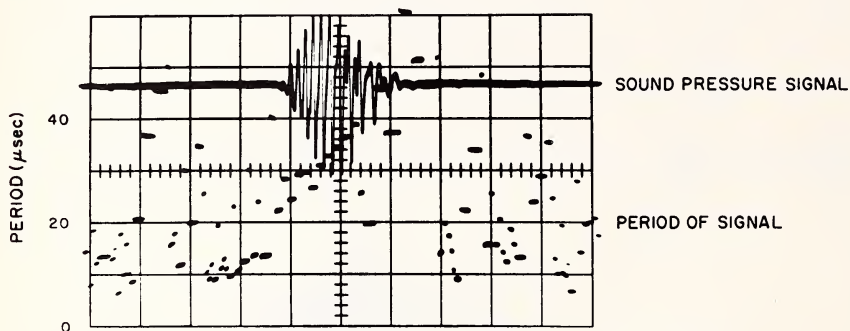


Figure 10. Myotis Lucifugus Pursuit Pulse (Pulse No. 5)

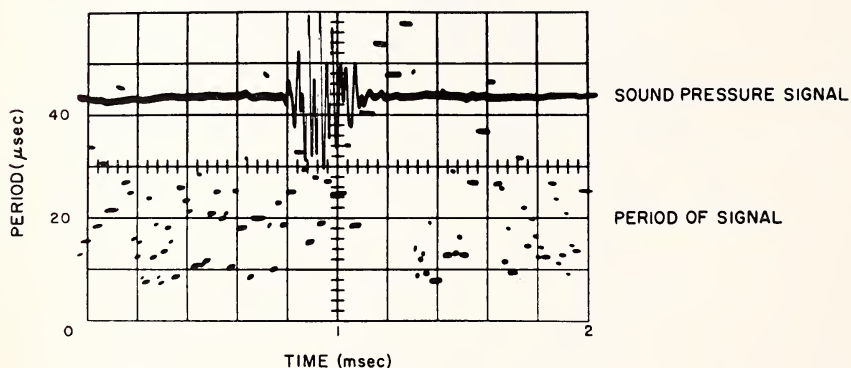


Figure 11. Myotis Lucifugus Pursuit Pulse No. 6)

The instantaneous frequency of these pulses is no longer defined in the relatively simple way that the instantaneous frequency of the three former pulses has been defined. The signals are no longer sinusoidal in shape, but contain a large amount of second harmonic.

If the instantaneous frequency of these signals is defined as the inverse of the time between the zero-crossings of the fundamental of the waveform, upper and lower frequency bounds can be defined. The frequency change for pulse no.5 is 40 kc down to 20 kc; the duration is .4 msec. The frequency range for the fundamental of pulse no. 6 is 50 kc down to 17 kc, the duration is .3 msec. Figures 12 and 13 illustrate three-dimensional drawings of the ambiguity diagrams for pulses no.5 and 6.

The ambiguity diagram of pulse no.5 has only 3 maxima. The ambiguity diagram of pulse no.6 has only 1 maxima.

Table 1 contains a summary of the parameters of the pulses and of the ambiguity diagrams. It is interesting that the one-Napier width of the envelope of the waveform in the $v = 0$ slice of the ambiguity diagram remains relatively constant for the various pulses. This means that the amount of spatial resolution that the bat has is relatively independent of the particular signal that it uses, out of the class of signals that are available to it.

Since the power of the echo decreases as the inverse fourth power of the distance from the bat to the target, it seems logical that the bat would be willing to accept some loss in range resolution during cruising in order to be able to use a more powerful signal. Suppose for example that the bat can detect a target at a distance of 1m. If a pulse that has the same energy is used when it is .1 m from the target, the echo energy is 10^4 greater!

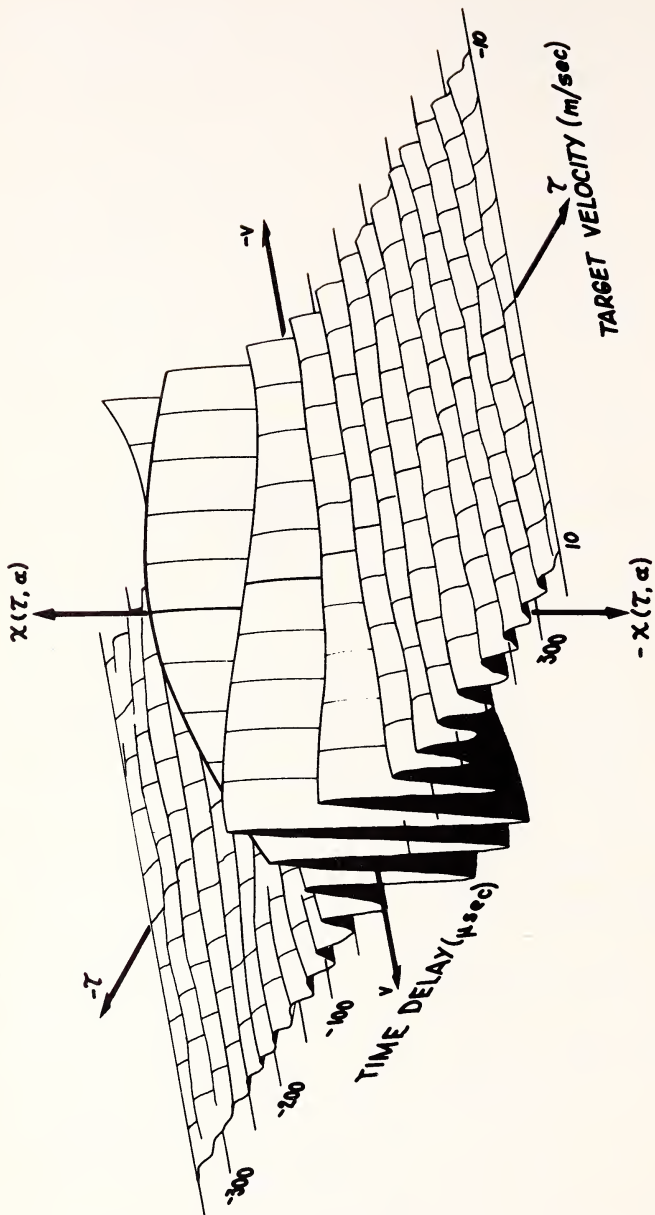


Figure 12. Pursuit-pulse Ambiguity Diagram for *Myotis Lucifugus* (Pulse No.5)

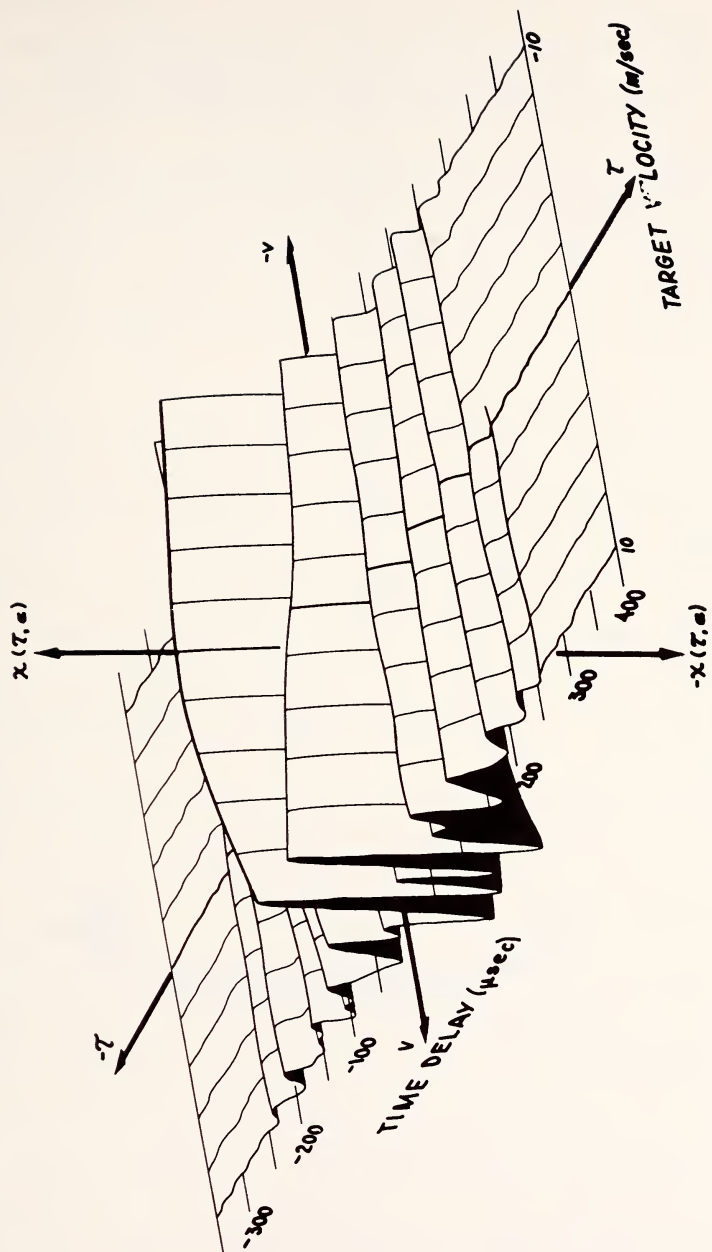


Figure 13. Pursuit-pulse Ambiguity Diagram for Myotis lucifugus (Pulse No.6)

TABLE 1. SUMMARY OF THE PARAMETERS OF BAT PULSES AND AMBIGUITY DIAGRAMS

Pulse Number	BAT PULSE			AMBIGUITY DIAGRAM		
	Duration msec	Start f kc	Stop f kc	v = 0 width sec	v = 10 width sec	maxima
<u>Myotis lucifugus</u>						
2	3.2	100	40	85	110	30
3	2.2	100	35	70	100	15
4	.8	50	30	85	110	7
5	.4	40	22	100	100	3
6	.3	(50)	(17)	125	125	1
<u>Lasiurus borealis</u>						
7	9.6	60	35	380	500	300

For the particular pulse train that has been analyzed, the duration of the cruising pulse is slightly more than ten times the duration of the pursuit pulse and the amplitude of the cruising pulse is about three times the amplitude of the pursuit pulse. Using these figures, the energy contained in the cruising pulse is 100 times the energy contained in the pursuit pulse. This means that if the bat had a signal-energy-to-noise-power-density ratio of 1 during cruising, he would have a ratio of 10^2 when he is on the final phase of the pursuit. Referring back to the ambiguity diagram for pulse no. 6, the type of pulse used in the final leg of the pursuit, it can be seen that with this very high signal-to-noise ratio, the position of the target is determined by only the very top of the central spike of this surface. This should lead to extremely good range accuracy.

LASIURUS BOREALIS

The bat Lasiurus borealis, commonly known as the red bat, grows to have a wing-spread of about 18 inches, and weighs between 10 and 30 grams.

The particular bat whose signals appear in this paper is a bat that was trained by Dr. Asher E. Treat and his family to catch grown moths in the wild. The tape recordings were made at Dr. Treat's summer home, at Tyringham, Massachusetts, during an evening when the bat was being thrown moths by several different people.

A microphone was situated in a fixed position near the house, pointing in the general direction of the bat's flight path. The same troubles with signal-to-noise ratio that were encountered with the signals from the Myotis were encountered with the signals from the Lasiurus, with the exception that since the signals were recorded in the free space outdoors, there were fewer multipath echo problems. The signal shown was chosen on the basis of having a good signal-to-noise ratio and is typical of the Lasiurus pulses.

Figure 14 shows the signal that is analyzed. The signal is designated pulse 7.

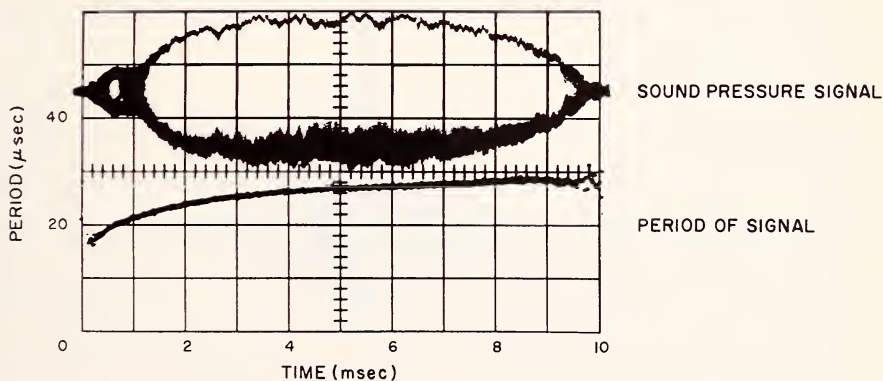


Figure 14. Lasiurus Borealis Cruising Pulse (Pulse No.7)

This is a cruising pulse; that is, it was emitted while the Lasiurus was in search of a target but had not yet detected it. This Lasiurus pulse is very different from any of the Myotis pulses. The frequency starts at about 60 kc and sweeps to 35 kc. The sweep in frequency is very non-linear and exhibits an almost-constant-frequency portion at the end of the pulse. The pulse has an extremely long duration, 9.6 msec, about three times the duration of the longest Myotis pulse. Figure 15 shows the auto-correlation function for this signal. Only half of the function is plotted since the function is symmetrical around $\tau = 0$. This auto-correlation function has more than four times the width of the auto-correlation function of the Myotis cruising pulse. The large number of peaks and valleys seem to indicate that this bat cannot make use of the fine structure information indicated in this auto-correlation function. This is not an exact statement, since with a high enough signal-to-noise ratio, the position of the target will be determined by the position of the very highest peak of the ambiguity diagram.

Figure 16 is a drawing of the ambiguity diagram. Since the fine structure differs so greatly from that of the Myotis slices, a different way of representing the ambiguity diagram for pulse no.7 was devised. For the Myotis, the entire ambiguity surface was shown, represented as an opaque surface, with the connections between the individual slices filled in.

For the Lasiurus, however, only the envelopes of the individual slices are represented, with the area inside these envelopes filled in with vertical lines representing the oscillations of the waveforms of the individual slices. The connections between the slices have been omitted because of the difficulty in drawing these lines and because there is not sufficient information to do an intelligent job of filling in the blank volume. Drawn in this way, some of the lower surface is also revealed, and one may observe the shape of the small sections that split off

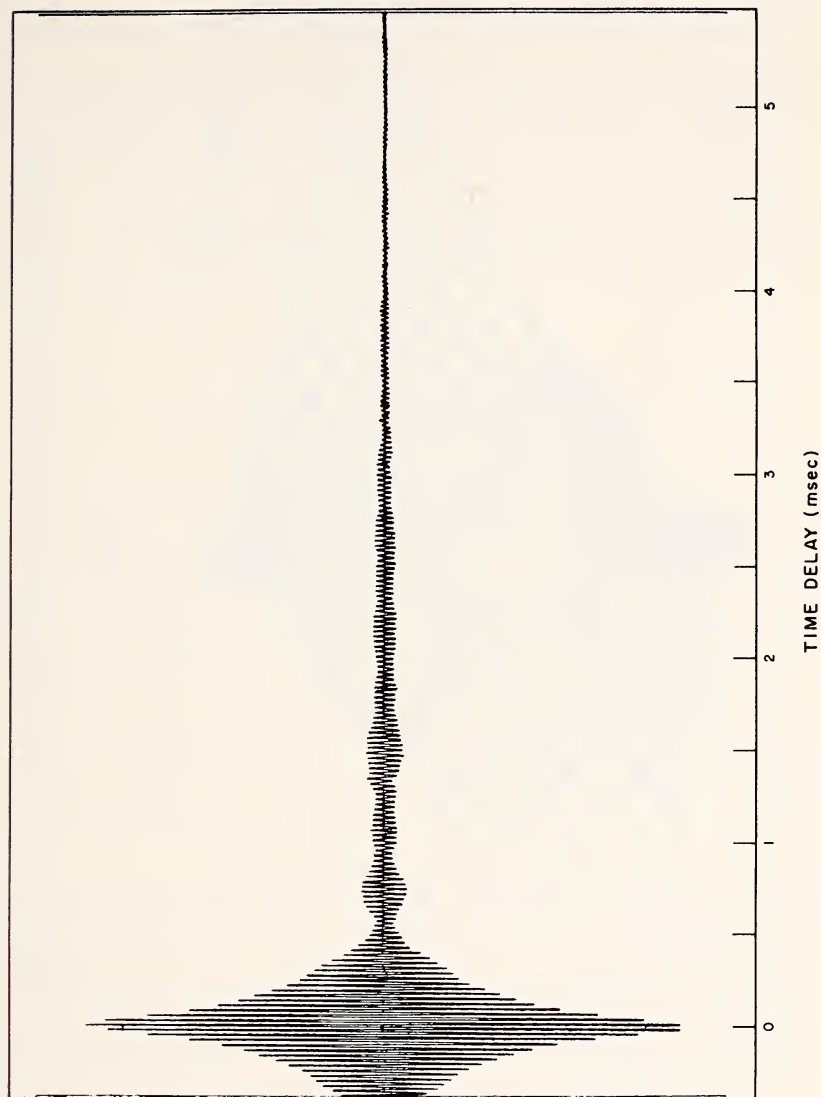


Figure 15. Cruising-pulse Auto-correlation Function for Lasiurus Borealis
(Pulse No.7)

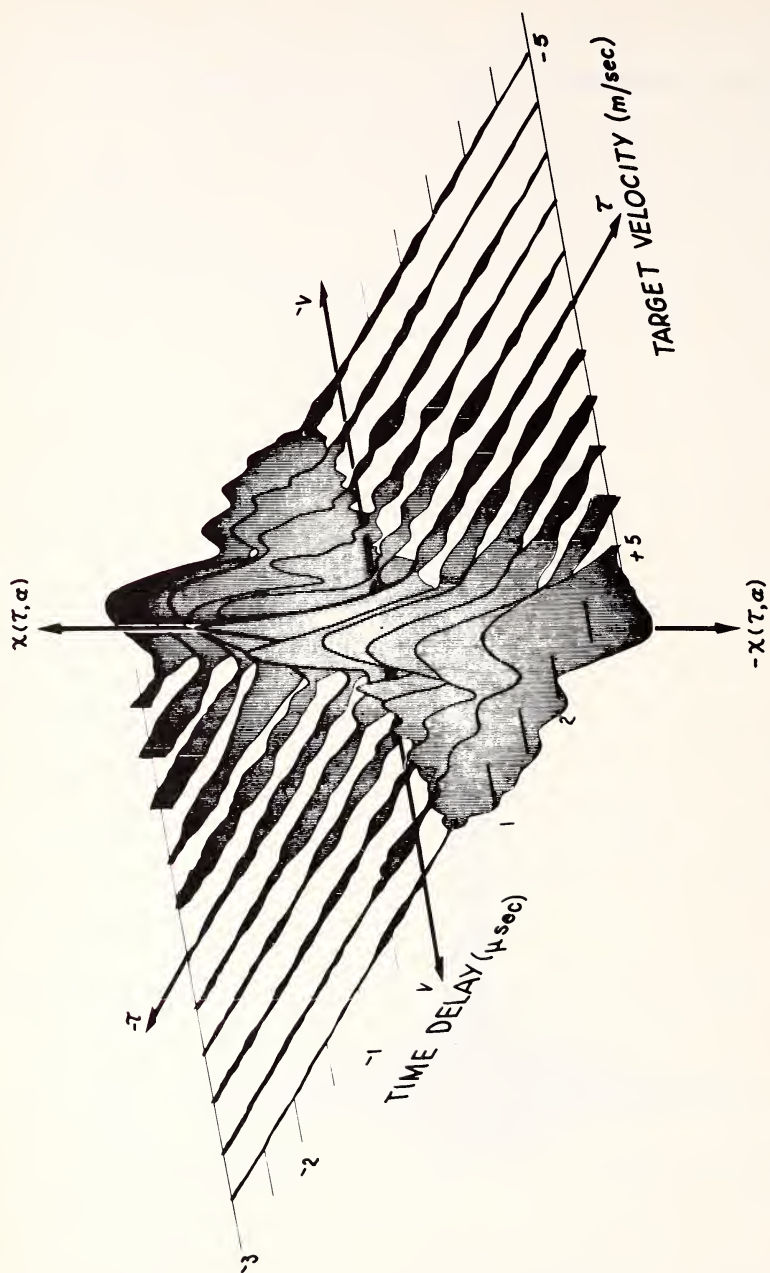


Figure 16. Slices of The Cruising-pulse Ambiguity Diagram for Lasiurus Borealis
(Pulse No.7)

beyond the Doppler-equal-to-zero slice, which would otherwise be hidden by the "mountain range" of peaks.

The distribution of the area of ambiguity is so different from that of the Myotis, that different scales are used on both the time-delay and the Doppler axis of the ambiguity diagram. The relatively restricted range for the Doppler scale, -5 to +5 m/sec, was used because of the limitations of the ambiguity diagram computer and not because the Lasiurus flies slower or catches slower targets than the Myotis. On the contrary, the Lasiurus usually flies about twice as fast as the Myotis.

Rather than exhibiting the relatively smooth behavior that the Myotis ambiguity diagrams exhibited, this ambiguity diagram splits into several sections off the Doppler-equal-to-zero slice. This is probably due to the fact that the signal does not have linear frequency modulation but has a very non-linear type of frequency modulation. The ambiguity diagram consists of the sum of the contributions of the various parts of the signal, as indicated by equation (8). When the signal is shifted from the $\tau = 0$ point, each portion of the signal is multiplied by a portion of the signal in its near vicinity. Therefore, the portion of the signal in the near vicinity of any portion is the only part that has a major effect on this portion's contribution to the area of ambiguity.

The width of the zero Doppler slice of this surface is 380 μ sec and the width of the -5 m/sec slice is 500 μ sec (the $\frac{1}{e}$ width). The range accuracy corresponding to a time-delay accuracy of 380 μ sec is 6.6 cm. Since this long pulse is used only for long range detection, it is not inconsistent that the bat does not have the excellent range measurement accuracy that the Myotis had.

The nature of the Lasiurus pulses changes greatly as the bat closes in on his target. Similar to the Myotis, the Lasiurus shortens his pulses until they are only

1 msec in duration when he is in the final phase of his pursuit. The Lasiurus, however, does not decrease the frequency of his signals as the Myotis does. He sweeps over approximately the same frequency range in the shorter length of time. The pursuit signals of the Lasiurus are not included here because ambiguity diagrams have not yet been computed for them.

DIRECTIONAL LOCATION WITH GAIN-DISPERSIVE ANTENNAS

Up to now only range and range-rate information have been discussed. A bat that is catching a target needs some form of azimuth and elevation information as well. It can obtain range information from the target echo delay. It can obtain azimuth information from the interaural delay of the echo, but the problem remains as to how the bat obtains elevation information.

One theory is that the bat wiggles his head back and forth to obtain several interaural delay measurements with different baselines. While the bats of one family, the Rhinolophidae, are known to wiggle their ears at a high rate, they use very narrow-band signals which would give them poor time resolution. High-speed photography of vespertilionid bats, in particular the little brown bats (Myotis lucifugus), in pursuit of thrown targets show no such head wiggling, while they clearly show that the bats have excellent elevation aim.

Another possible explanation is that the bat is using the gain pattern of his ears to determine the elevation of his target. The bat's ears have a different Fourier system function for different angles. In other words, the gain pattern of the bat's ears varies as a function of frequency. The bat must decide from what angle his echo is returning by determining through which system function its signal most probably passed.

The problem reduces to a problem of determining the impulse response of a linear system from the noisy output of the system, given the form of the input signal and the class of functions to which the impulse response belongs. By assuming additive Gaussian noise in the reception system that is independent of the position of the target, the problem can be treated in the same framework as the problem of determining range and range-rate. The best that an ideal receiver can do is to compute the a posteriori probability distribution for the elevation angle and the time delay of the target, given the received signal. An antenna function is defined which is the complex Fourier system function for the antenna at the angle θ . A signal function is then defined that describes the operation of the time delay and elevation measurement system. This signal function is similar to the signal function described previously except that this signal function depends on the form of the antenna as well as the form of the transmitted signal.

Figure 17 shows the model used for this analysis. The echo signal comes into the receiving antenna at an angle θ . After the signal is received by the antenna, white Gaussian noise is added. The received signal $y(t)$ therefore consists of two parts: the transmitted signal $s(t)$ passed through a linear filter (the antenna) and the additive, white Gaussian noise.

$$\text{Eq.13} \quad y(t) = n(t) + \int_{-\infty}^{\infty} s(\eta - \tau) h(\theta, t - \eta) d\eta$$

where

$s(t)$	= transmitted signal
$n(t)$	= additive Gaussian noise
τ	= time delay associated with the range
$h(\theta, t)$	= impulse response of antenna at angle
$y(t)$	= received signal

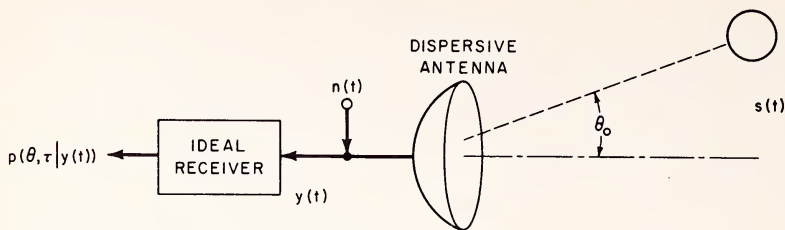


Figure 17. Gain-dispersive Antenna Model

Several signal functions have been calculated using hypothetical signals and hypothetical antennas. It turns out that the signal function is dependent only on the bandwidth of the signal and not on its shape. Figures 18 and 19 show the form of the signal functions and the corresponding likelihood functions for a square window-function-antenna with the target 30° and 60° off axis. (This is an antenna that has a constant sensitivity over a square aperture). The signal that was used was an impulse, white noise, or an FM signal. Notice that even with the signal function obtained for a target 60° off axis at a reasonable signal-to-noise ratio ($\frac{|S(\omega)|^2}{N_0}$) such as 100 (20db) angular localization can be very good.

Figure 20 shows a three-dimensional graph of the signal function. This shows how well the range and elevation of a target can be simultaneously measured.

If we allow our imaginations to wander slightly we can hypothesize an antenna with the sensitivity shown in Figure 21.

Two signal functions have been calculated for this type of antenna and are shown in Figures 22 and 23. With this modified antenna there is a great improvement in angular localization. This is effectively an array antenna.

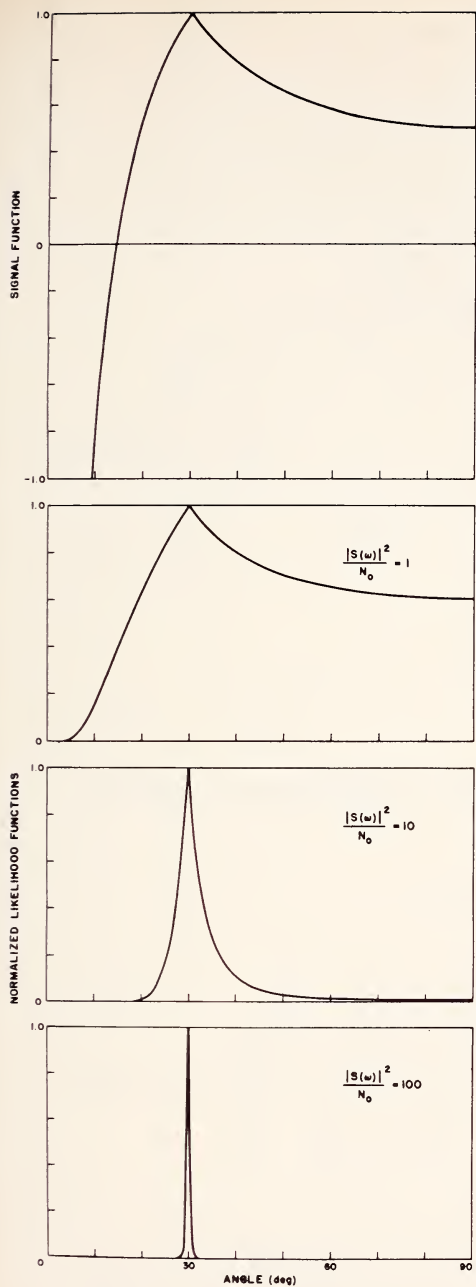


Figure 18. Signal Function And Likelihood Functions for a Square Window-function-antenna

$$\tau = 0, \theta_0 = 30^\circ$$

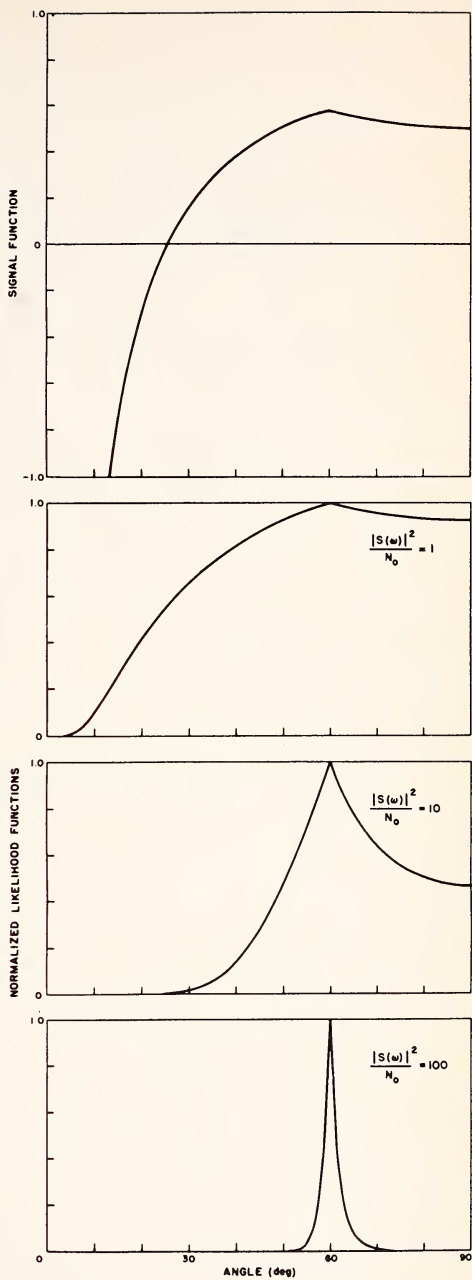


Figure 19. Signal Function And Likelihood Functions for a Square Window-function-antenna

$$\tau = 0, \theta_0 = 60^\circ$$

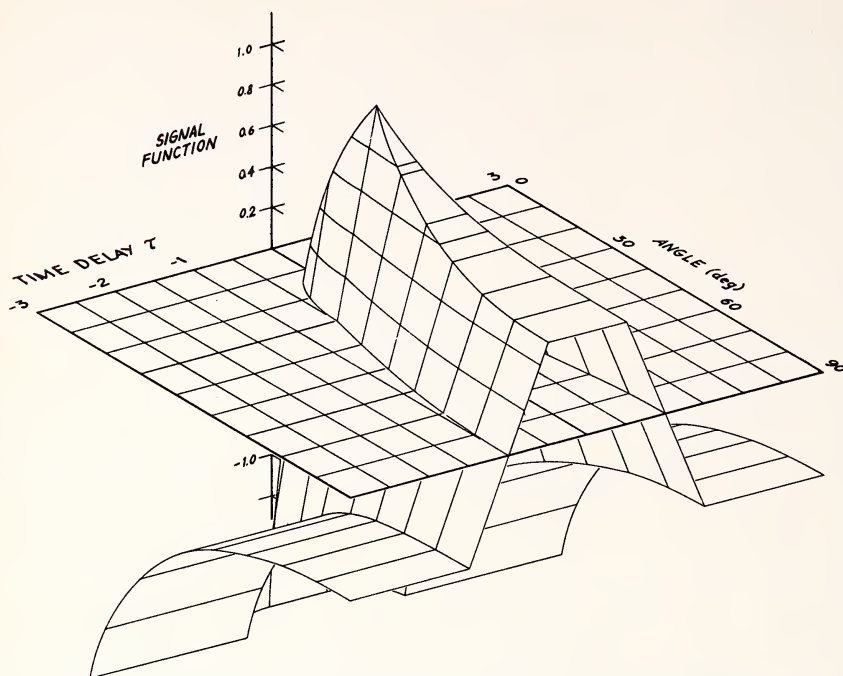


Figure 20. Three Dimensional Graph of The Signal Function of a Square Window-function antenna

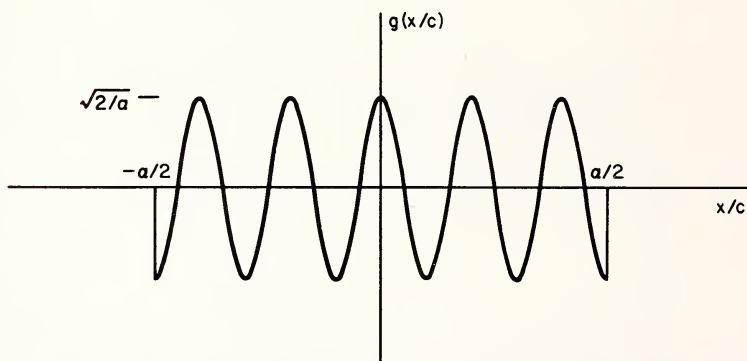


Figure 21. Window Function for a 5-cycle-cosine Window-function Antenna

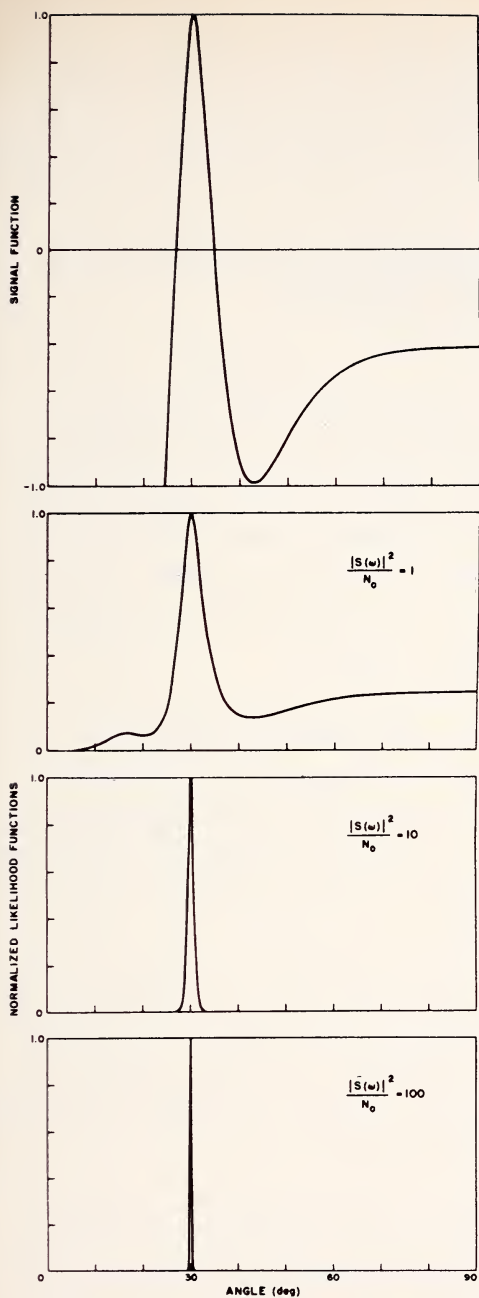


Figure 22. Signal Function And Likelihood Functions for a 5-cycle-cosine Window-function-antenna
 $\tau = 0, \theta_0 = 30^\circ$

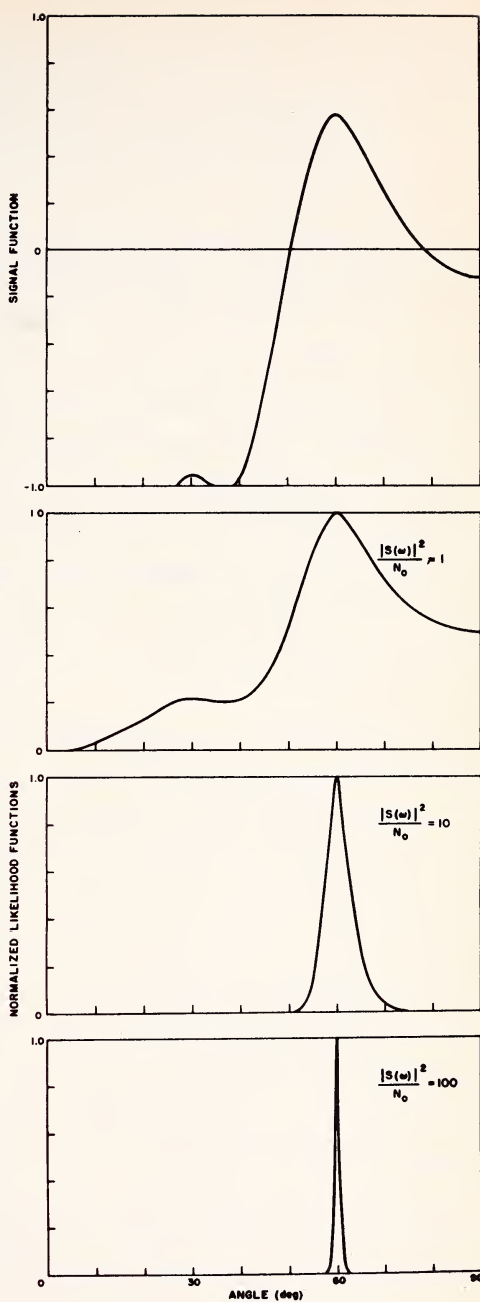


Figure 23. Signal Function and Likelihood Functions for a 5-cycle-cosine Window-function-antenna
 $\tau = 0, \theta_0 = 60^\circ$

DISCUSSION

par

J. C. LEVY

Caractères généraux des signaux d'orientation acoustiques, et performances des sonars, dans l'ordre des Chiroptères.

Je n'avais fait qu'une remarque au sujet de ce remarquable exposé, mais par la suite, la question avait été reprise dans l'exposé du Dr. CAHLANDER, d'une façon beaucoup plus précise et plus complète que je ne l'avait fait. Je me bornerai donc à rappeler que la grande durée des impulsions de localisation à fréquence constante du Rhinolophus, pouvait permettre la mesure de l'effet Doppler, et que seule la courte modulation de fréquence qui marque la fin de cette impulsion pouvait permettre la télémétrie précise.

Le problème avait été traité par le Dr. CAHLANDER, au moyen des fonctions d'incertitude. Un autre cas étudié par le Dr. CAHLANDER, est celui des Vespertilionidae, dont l'impulsion d'écholocalisation plus brève, est modulée en fréquence. Dans ce cas, il existe une incertitude entre la télémétrie et la vitesse radiale.

Selon ce principe, un objet éloigné donne à l'animal la même impression qu'un objet plus proche mais s'éloignant de lui. Il est alors facile de démontrer que tous les objets correspondant à la même incertitude distance-vitesse, correspondent à un objet, dont la distance est connue un temps donné T après celui de la détection.

En effet, une augmentation de la vitesse d'éloignement de 20 mètres secondes, donne à l'animal la même impression qu'une augmentation de distance de 9 centimètres (rapport du Dr. CAHLANDER, Fig. 4)

Le temps T est alors de :
$$\frac{9 \cdot 10^{-2}}{20} = 4,5$$

Ce temps d'extrapolation très faible semble ne servir qu'à corriger le retard du trajet retour de l'écho, de façon à donner à l'animal, malgré la vitesse du son, une représentation instantanée de l'objectif.

DISCUSSION

by

R. S. MACKAY

Dr. Batteau is to be complimented on his ability to produce generalized formulations. The transformations he has indicated are somewhat different from the ones to which we are accustomed, but they appear quite proper and stimulating. Some of the considerations in my own paper, scheduled for later in the week, take up the same kinds of questions from quite a different viewpoint, and might be considered as supplementary to the present paper.

In considering the enormity of the task of the animal in sorting out the functional relationships involved in making appropriate transformations, I was led to consider the kinds of information required and how they might be used. What might be considered a parallel situation has been described for color vision, in which an apparently limited amount of information sometimes effectively provides a broad spectrum of results. I am referring to the possibilities of producing a "proper" full colored image using only two groups of wavelengths. These effects were emphasized by Land a few years ago, though they had been known before this. One wonders if information about a few sound frequencies (plus knowledge of the incident spectrum) might in some cases similarly provide for an extremely varied result. In the vision case, it would appear that basically the effects are due to the possibility of one color modifying the appearance of an adjacent color. The "perfect pitch" attributed to some musicians suggests that in humans one tone does not much modify the apparent pitch of a simultaneously sounded tone (though a mechanical stimulation of the skin certainly modifies the sensation of an adjacent stimulation). Experiments along these lines could be instructive. It may

turn out that a single tone from an animal in combination with "white noise" (or ocean background noise) gives much more useful information than expected.

All the transformations (equations # 2 on) contain attenuation terms and, though the use of directional receivers is included in equation 5, one aspect could be confusing. The strength of a returned signal depends on the orientation of the object, being close to zero for a flat object several wavelengths across not oriented perpendicularly to the sound beam. This does not detract from the analyses given, but does indicate the complexity of the actual transformation being made.

His comments on sweeping frequency seem especially relevant. Those who have watched motion pictures from ultrasonic image tubes (e.g., the work of Smyth in England or Jacobs in America) will appreciate the motion and possible confusion of standing waves and interference patterns. A sweep in frequency (or use of a broad-band signal), seems to human senses like a way to blur or average this confusing structure, but it might be used by other animals. The wrinkling of the head of captive beluga whales is very noticeable and may constitute a variable focus acoustic lens action; it could serve a function related to the above at a fixed frequency, or it could be for concentrating on different ranges or sizes of objects.

With regard to his discussion of planar and nonplanar systems and frequency functions, I fully agree. But I can also visualize a number of useful sonar cases where phase information is a valuable extra parameter that the animal should use, but in which situations the information is also contained in the relative amplitudes of a number of frequency components. The animal could function in these cases on frequency information alone, and could choose signals to emphasize these effects. Experiments to distinguish the type of functioning in various animals will be useful. In my own paper, I repeat his thought that a frequency analysis alone may not be enough to describe animal performance.

That one can tell direction of a pulse with one ear because appearance depends on direction is very interesting. To work with a random sound (e.g. noise or a pure tone), I imagine one ear would have trouble. Is information available as to how far this can be carried?

At a local blind school, the children often walk by the teachers and call them by name, even though the latter are silent and motionless. When asked how they sense their presence, the children reply that they "hear" them, though they can give no details. This fits in well with Dr. Batteau's final comments.

Some other analogs with visible light considerations might also be instructive. Surface irregularities are examined with great precision by the interference patterns they produce, and so on a larger scale, the same might be done by sonar. Also, if one observes the reflection of a laser beam off of a random surface, one sees a twinkling whose frequency depends on observer velocity; being coherent, a similar thing might be done with sounds.

DISCUSSION

by

M. FEDERICI

The author gives an extremely interesting and thought provoking view of the operation of sonar in animals.

A comparison with the system theory of sonar equipment, as known to engineers, appears to be a useful comment.

A sonar system is composed of a signal producing system, a transmitting array which insonifies space with the signal, a receiving array which receives the reflected signal, and a signal processing system which extracts information from the reflected echo.

I should like to stress at the outset the difference between sonar systems used by engineers and sonar systems as applied to animals.

For a long time the use of sonar was greatly limited. It was employed to ascertain the presence of an obstacle (usually a submarine) in water, and as the range was insufficient for tactical purposes, all efforts were dedicated towards increasing this range. Only recently because of an increase in power and directivity and a better knowledge of acoustical propagation, ranges have become greater and predictable, and the engineer has been able to turn away from this overpowering problem to put his mind to that of obtaining more information from echoes. In animals the emphasis is obviously the reverse. Ranges are small, path attenuation is not so important, and the shape of signals and detection procedures are directed towards obtaining a maximum amount of information from echoes.

Techniques in sonar have now progressed so far that the sonar engineer, even if he has not solved all the problems, can at least formulate them in a general way.

Translating the considerations of the author into the usual language of the sonar engineer, we may first consider reception by a single transducer. If we indicate by p the sound pressure at a given frequency ω produced by the transmitting system at a given point (say one yard from the transducer) in space, and with p_r the sound pressure received at that same point at the same frequency as reflected by the obstacles, the relation can be written as:

$$\frac{p_r}{p_t} = y(j\omega)$$

The term $y(j\omega)$ includes the effect of all the obstacles in a given situation.

For instance, in the simplest possible case in which the obstacle is a single rigid sphere of radius r_0 , at a distance R from the transmitting system:

$$y(j\omega) = \frac{e^{-j2KR}}{KR^2} \sum_{n=0}^{\infty} (-1)^n \frac{(2n+1)\mu_n(Kr_0)}{\mu_n(Kr_0) + j\nu_n(Kr_0)}$$

where U and V are Bessel functions. (1)

Of course this formule is true if the sphere is entirely rigid and has none of its own resonant frequencies as often happens, in which case additional terms are introduced.

If the number of obstacles is great, and the effect of each is independent from the effect of the others, one can write:

$$y(j\omega) = y_1(j\omega) + y_2(j\omega) + \dots$$

If the sound pressure due to the transmitter is not sinusoidal, but any function of time, the usual laws of linear systems apply, and the pressure reflected can be obtained by a convolution integral:

$$p_r(t) = \int_0^{\infty} p_t(t-\tau) h(\tau) d\tau$$

where:

$$h(t) = \frac{1}{2\pi} \int_{-\infty}^{+\infty} y(j\omega) e^{j\omega t} d\omega$$

is the impulsive response of the reflecting system.

The reflected pressure therefore depends upon the signal transmitted and the impedance of the obstacles. Thus, it is considered as a

(1) Stenzel = Berechnung von Schallvorgängen

linear transducer which accepts as input the transmitted pressure and gives as output the reflected pressure.

Now if we call p_t the outgoing pressure, p_r the reflected pressure, G_{tt} the power spectral density of p_t , and G_{tr} the crosspower spectral density of p_t and p_r :

$$|y(j\omega)| = \frac{|G_{tr}(\omega)|}{G_{tt}(\omega)}, \text{ phase of } y(j\omega) = \text{phase } G_{tr}(\omega)$$

Two cross correlation operations are sufficient to obtain phase and amplitude of the linear operator due to the environment.

However, the signal received in a sonar is normally contaminated by noise, and the operator is interested in identifying a given signal (say the presence of a target) at a maximum range. In this case, the best procedure consists of using a signal processing method that will give the greatest ratio of peak signal to root mean square noise in the output. This means using filters matched to the expected signal or alternately carrying out cross correlations between the received signal and all the expected signals rather than between the transmitted and the received signal. The expected signal which gives the maximum value of cross correlation is the most likely received signal. Of course the operator is interested not only in ascertaining if a signal has been received but in the type of signal received. For instance, a change in range and Doppler produces a change in the received signal. In this case the engineer will locally provide a double multiplicity of local signals differing in range and in Doppler, and the result of the correlation of this double multiplicity of signals with the received input will be a double multiplicity of correlation functions. The peaks of those correlation functions can be represented on the Z axis. (°) The surface thus obtained, which is called an ambiguity function, depends on the type of signal employed, and gives relevant data useful in the choice of the type of signal to be used.

The possibility of detecting small variations in Doppler and range depend upon the shape of the ambiguity function and of course upon the noise present in the system which introduces an error in the measurement of the correlation function.

The engineer is interested not only in Doppler and range but also in the shape of the target, its size, etc.

If he still wants to get the best output signal to noise ratio, he should follow the same procedure, that is to provide locally replicas for all possible signals received, and carry out crosscorrelation between these signals and the received signal. If on the other hand signal to noise ratio is ample, other methods can be resorted to similar to the one

(°) Range and Doppler on the x and y axis.

first suggested. This examination of the question is not complete because so far we have only considered one part of reception. Generally, reception is carried out by means of a receiving array, and the matched filter technique must be extended to a multiplicity of sound pressures from each transducer of the array.

Each sound pressure is correlated with the sound pressure expected for a given bearing and elevation, and the sum of all correlation functions is examined. Again the concept of ambiguity can be applied.

Of course the bandwidth of the signal employed is extremely important.

For a long time sonar systems worked with C W pulses on a very narrow band indeed. F M and PRN systems are now common with a larger bandwidth, but a much greater amount of information could be obtained by widening the band still more. This is a problem that has not yet been solved because sonar transducers in the past have been principally narrow band, and it is only lately that the introduction of PTZ has permitted building transducers with a q as low as 2. Also the selective attenuation of water limits the band. However, narrow pulses with a very wide spectrum obtained with the explosion of a TNT charge are commonly used to measure propagation properties in water, reflection from limiting surfaces, etc.

The advantages derived from the use of these pulses depend of course, on the shape of the sound transfer function. Total knowledge of the function requires the transmission and reception of a bandwidth which extends from zero to infinity. In the case of such a simple obstacle as a sphere, a knowledge of the radius from the echo can only be deduced if we go down to wavelengths comparable to the radius.

If we reflect now on the approach taken by the author when he considers the stimulus which results in environmental sound as a communication channel and the perceived result as a message, we can see that what has been said before is quite compatible with this point of view.

All the expected signal, (produced by the transformation created by the environment operating on the transmitted signal) can be considered as messages, and the concepts of information theory can be applied to it.

The example given of the time encoding provided by the ear bears great similarity to the operation carried out by a directive array. The sound field due to a steep pulse, reaching a linear directive array from any bearing different from normal direction, gives a succession of delayed pulses at the output of the array, and the delay gives the required information on bearing.

Again, the two "philosophical" statements of the author are quite true, and their counterpart in the sonar system (and information theory) can be demonstrated mathematically.

The first derives directly from the definition of the information received as:

$$\log \frac{\text{probability at the receiver of the event after the message is received}}{\text{probability at the receiver of the event before the message is received}}$$

The information received from a message already known is zero. The second statement is again quite true for the signal treatment normally employed in sonar systems.

After a signal has gone through a matched filter, the shape of the signal is lost and only the selective stimulus remains. The stimulus is due to the peak of the correlation function, its selectivity is due to the fact that the peak appears in one and only one matched filter which is the filter corresponding to the signal received.

In considering the recognition process an electrical engineer would classify networks into two classes - networks of minimum phase in which loss and phase are entirely dependent on one another and a definition of the amplitude response of a realizable network also defines phase; and non-minimum phase shift networks which, besides additional phase rotation. In the first case, response can be reconstructed from amplitude response which contains all the information. In the second case, only the minimum phase response can be reconstructed. It is therefore true that power spectral density does not furnish enough to obtain the phase factor as we said before by carrying out an additional cross correlation operation. The ratio between the "cross correlation" of the transmitted signal entirely defines the sound transfer function of the environment.

However as the author rightly says, the autocorrelation function and the spectral density of the received signal do not give all the information describing the signal, which of course is only obtained if amplitude and phase of component are specified. This is a familiar occurrence to a communication engineer who is often called upon to deal with signals of a widely different nature having the same spectrum distribution but different phases for each component of the spectrum.

So far the author's observations are extremely to the point. Interference patterns due to the movement of the object or to the change in frequency are extremely important, and have not received due importance in sonar work. Their significance begins to be realized only now. Also, the sound coloration is, of course, important. As I said, in sonar work we are unable as yet to transmit very wide bands. As techniques progress this is certainly one of the points which sonar engineers should turn their attention to so that sonar capabilities may be increased.

In concluding it may be said that knowledge of the use of sonar in animals may inspire the sonar engineer to invent many interesting and novel techniques. In the same way a knowledge of the methods of signal processing used by the sonar engineer may help biologists to shed light on the mechanism employed by animals for the same purpose.

DISCUSSION

par

P. GOURLAY

L'auteur procède tout d'abord à un rappel sur la théorie du sonar actif, en introduisant la notion de directivité, et la possibilité de mesure de la vitesse de l'écho par l'effet Doppler.

L'expression mathématique du signal reçu $H(s)$ sous la forme $H(s) = P(s) \cdot T(s)$ permet de poser dans sa généralité le problème de correspondance entre le signal émis et le signal reçu qui a subi la transformation due au milieu et d'où il faut extraire l'information.

L'exemple donné, concernant l'oreille qui possède une directivité en azimut et en élévation, explique bien la détermination de la direction d'un écho, mais n'indique pas clairement par quel mécanisme est obtenue l'information distance.

L'auteur revient ensuite sur le problème de l'extraction de l'information lorsque l'on connaît le signal émis. Il paraît nécessaire de conserver toute l'information reçue, en amplitude, fréquence et phase, si l'on veut faire une analyse poussée du signal à la réception.

Examinant enfin les 3 types fondamentaux de signaux possibles, modulation de fréquence, impulsion et bruit blanc, l'auteur conclut à la supériorité de l'impulsion en ce qui concerne la capacité d'information.

CRITIQUE:

Il me semble nécessaire de séparer nettement les systèmes de détection et ceux de télécommunications.

- un système de détection doit permettre de détecter la présence d'un objet, de le localiser et de le classer.

- un système de télécommunication doit assurer une liaison entre une source d'information et un utilisateur.

L'auteur a essentiellement examiné le cas du système de détection *.

En se limitant au cas du système de détection, on peut tout d'abord noter les performances principales:

- la portée et le volume de surveillance
- la précision (en distance, en direction et en vitesse)
- l'âge et la cadence d'information
- le pouvoir de classification.

Un objet quelconque ne peut être décelé que s'il modifie son environnement; on peut observer cette modification de 4 façons:

- 1) en détection passive, l'objet émet de l'énergie que l'on détecte et analyse,
- 2) en détection semi-passive, l'objet perturbe un champ naturel (ex.: vision),
- 3) en détection semi-active, on crée un champ par une source séparée du récepteur, et l'objet perturbe ce champ,
- 4) en détection active, on détecte la modification de champ apportée par l'objet, le champ étant créé au niveau du détecteur.

En restant dans le domaine de l'acoustique, il apparaît que les animaux doivent utiliser les principes 1) et 4).

Dans ces deux cas, c'est le pouvoir de localisation et de classification des animaux qui paraît le plus surprenant. En effet, la portée observée paraît moyenne et les études actuelles de traitement du signal à l'émission (optimisation du signal) englobent les différents types de signaux observés chez les animaux

* Il semble que les dauphins n'utilisent pas le même type de signal lorsqu'ils explorent le milieu où ils se trouvent (série d'impulsions) et lorsqu'ils parlent entre eux (modulation de fréquence).

(modulation de fréquence, impulsion, bruits). D'autre part, l'obtention d'une grande précision angulaire est liée pour une gamme donnée de fréquences aux dimensions de l'antenne de réception. La limitation chez les animaux est évidente, à moins qu'ils n'utilisent des lentilles du type Luneberg.

Par contre, les études de R.-G. BUSNEL ont montré que le dauphin est capable de détecter la présence de fil de diamètre inférieur à un millimètre et de reconnaître un grand nombre de bruits. C'est l'analyse de ce pouvoir de classification qui me semble la plus enrichissante, aussi bien pour l'application aux sonars humains que pour la compréhension du comportement des animaux.

L'animal procède sans doute par comparaison entre le signal reçu et une suite de modèles faisant partie de son dictionnaire des objets, ce dictionnaire étant enrichi de toutes ses expériences antérieures. Il dispose ainsi de critères de classification lui permettant de sélectionner l'objet intéressant dans son environnement. On voit donc que le dauphin possède un "senseur" relativement peu puissant mais que son cerveau lui permet grâce à sa fonction mémoire et à ses possibilités d'adaptation, d'avoir une connaissance fine de son milieu.

THEORIES OF SONAR SYSTEMS
IN RELATION
TO BIOLOGICAL ORGANISMS

by
J. W. R. GRIFFITHS

1. Introduction

An engineer's approach to animal sonar systems will usually be quite different from that of a zoologist or animal psychologist. Engineers are generally not intrinsically interested in the animals themselves but in what they can learn from a study of their behaviour. It might be said, with some justification, that engineers have been very slow in making use by analogy of known abilities of certain animals, perhaps the most glaring example being the failure to study more closely the obvious navigation abilities of the bat. As long ago as 1793 Spallanzani, by a series of remarkably thorough experiments proved fairly conclusively that bats used their ears for location; but because the sound frequencies which they used were above the range of the only sound measuring instruments available - his own ears, - he was unable to detect the presence of these waves and his work was more or less ignored. In fact it was well into this century before sound location systems were developed at all and not until 1938 was it established by Griffin and Pierce that bats in fact produce ultra-sonic waves. Blind people have, of course, always made use of audio stimulus for navigation but they are often not aware of exactly how they do this and many will deny that they are in fact only using their ears -

rather that they are able to 'feel' the presence of nearby objects. It needed the painstaking and exacting experiments of Supa, Cotzin and Dallenback to explode this myth and to prove conclusively that sound is in fact the *modus operandi*.

In the early years of Radar and Sonar, attention was concentrated on the single frequency pulsed system using a narrow beam to determine bearing and/or elevation. Some studies were made of continuous wave systems and frequency modulated systems but except in special circumstances these alternatives seemed to have little to offer. In recent years the situation has changed somewhat probably because on the one hand more and more is being asked of the systems - higher resolution, faster detection, automatic signal processing - and on the other hand the tools are becoming available with which to supply these needs. Data processing and the computer industry have expanded very rapidly in the last decade and the advent of the transistor and now the integrated circuit has considerably changed the picture. Because of the small size and low power consumption of these devices highly complex equipments are no longer ruled out simply on the basis of cost and size. Special purpose computers can be built to process the raw data available from the Radar or Sonar equipment and to try to make

better use of the information in the signals received (for example see references 4-8).

We are a long way from knowing how animals, and in particular the human, interprets the various sensory stimuli he receives and it is possible that if more were known about these naturally evolved systems it would be possible to design more efficient radar and sonar equipments. I am not suggesting that such a possibility has not been examined before; for instance, there was an obvious close connection between the study that Leslie Kay was making of the bat's locations system⁽⁹⁾ and the successful blind aid which he has recently developed⁽¹⁰⁾.

However the remainder of this paper will not be directly concerned with a discussion of how any particular animal's sonar operates but will be discussing what appears to be the limitations and controlling factors of the general radar or sonar system.

To measure the efficiency of a system a criterion or standard must be decided upon. Simple detection of signals is not usually sufficient in itself and further information such as range, bearing, elevation, velocity etc. is needed to help in classification. Radar clutter and sonar reverberation are both forms of signal but they are usually unwanted forms and it is necessary to distinguish the

wanted targets from the interference.

2. The formation of Acoustic Images.

When we use our visual sense for moving around in everyday life very detailed information is available about the surroundings - there are something like 10^8 receptors in the human retina each of which is capable of conveying many levels of intensity - but we process this information at a relatively slow rate, a rate which appears to be limited by our signal processing unit. It is perhaps not too much to expect that animals that navigate by sonar may have fairly detailed information too, but in some other form.

What then, are the possibilities of forming sonar images analogous to the forming of images by a normal lens? Although sound waves and light waves are fundamentally different there are in fact many similarities and it is perfectly feasible to form an image of an acoustic scene - it just proves difficult in practice. One main problem is the rather large wavelength that it is normally necessary to use in sonar systems. Radiated sound is attenuated fairly rapidly in most media and this attenuation increases very rapidly as the frequency of transmission is increased. This factor limits the highest operating frequency of a sonar system and it is usual to find the frequency chosen in the range 10 kc/s to 1 Mc/s, the



Acoustic image of
cylinder.



Light image when
illuminated from
direction of camera
only.



Light image, diffuse
illumination.

Figure 1. Comparison of acoustic and light images of a solid
cylinder.

higher frequency range being of any value only for very short range equipments. At 100 kc/s the wavelength is about 3.5 mm in air and about 15 mm in water. Thus the physical size of the lens must be fairly large if it is to contain a substantial number of wavelengths. In contrast a 1 cm optical lens would be of the order of 10^5 wavelengths across.

Mainly because of this difference in wavelength the acoustic image of a scene looks quite different from the optical image of the same scene. A photograph of such an acoustic image is shown in figure 1 and it can be seen to differ considerably from the normal photographs alongside. Incidentally it will be noticed how much we rely for recognition in the visual situation, on the fact that objects are illuminated from many different directions.

The acoustic image mainly comprises the specular reflections i.e. the highlights of the object whereas the light image also contains a substantial contribution from light scattered by the surface of the object. In fact in observing an object the eye practically ignores the highlights in a way the camera cannot do and recognition of shape and hence identification is controlled mainly by the scattered light. Present electrical systems are not sufficiently sophisticated to adapt themselves to the various situations as can

the human eye and when one considers the way in which the eye can rapidly focus to a different scene and the problem of three dimensional displays one realises the difficulties of this deceptively simple analogy.

A further difficulty is in the practical realisation of the acoustic equivalent of the retina. If the sound image is to be communicated to an operator - or even to a machine - the sound signals in the image plane have to be transduced into a form suitable for presentation. This usually means conversion into electrical signals and so to a light image which can be interpreted by an operator. Several working acoustic cameras have been produced based on the television camera principle^(11,12) i.e. an electron beam scanning an array of sound sensitive devices. Unfortunately glass is not transparent to sound and so the piezo-electric material has to be exposed to the media (water or air), on one side and a vacuum on the other, presenting difficult construction problems.

3. Fourier transform or Signal Processing Approach.

A sound image can be formed in the more conventional manner by carrying out a Fourier transform of the sound intensity distribution across an aperture. It is necessary however to code the illuminating signal in some manner so that the signals coming from different ranges can be distinguished and of course the simplest method of

of doing this is by sending out periodic pulses. The normal Sonar system is in fact carrying out the process described above. The transmitter is pulsed and so the signals coming from different ranges can be recognized by their time delay. The Fourier transform is less obvious but this is obtained by the normal sonar transducer as it is rotated to delineate the sound coming from different directions. The transform is more obvious in the case of the electronic scanning system which scans a sector very rapidly as the signal is being received. The resolution of a system in terms of bearing and elevation can be shown to be a function of the aperture size in wavelengths and so it does not seem to matter materially whether the sound field information is processed by imaging or by the normal techniques - it is purely a matter of practical convenience.

It seems unlikely that animals using sonar for navigation use any image forming technique similar to the retina. Physiological evidence suggests an aural system similar to the human's, except that it is sensitive to much higher frequencies. The bat, as is well known, generates frequencies of the order of 30 - 100 kc/s i.e. of wavelengths 3.5 mm to 12 mm, so it is obvious that the physical dimensions of the transducers is not large in terms of the number of

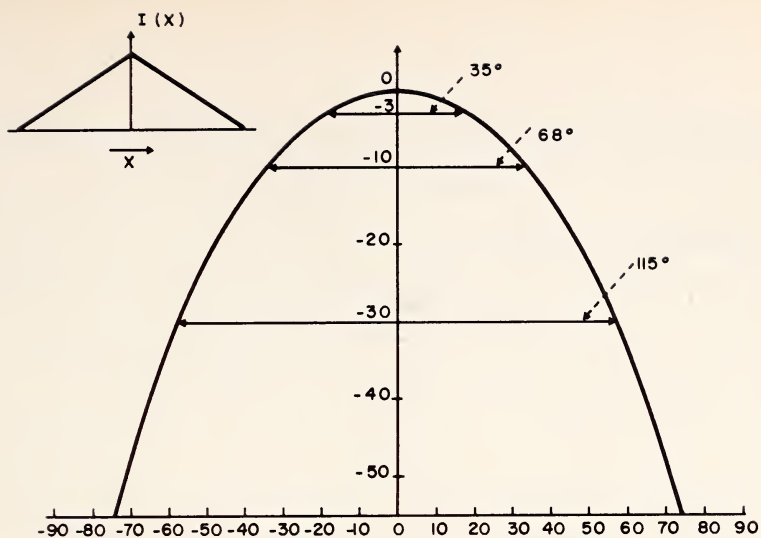


Fig. 2 — Directivity function for a linear taper illuminating function

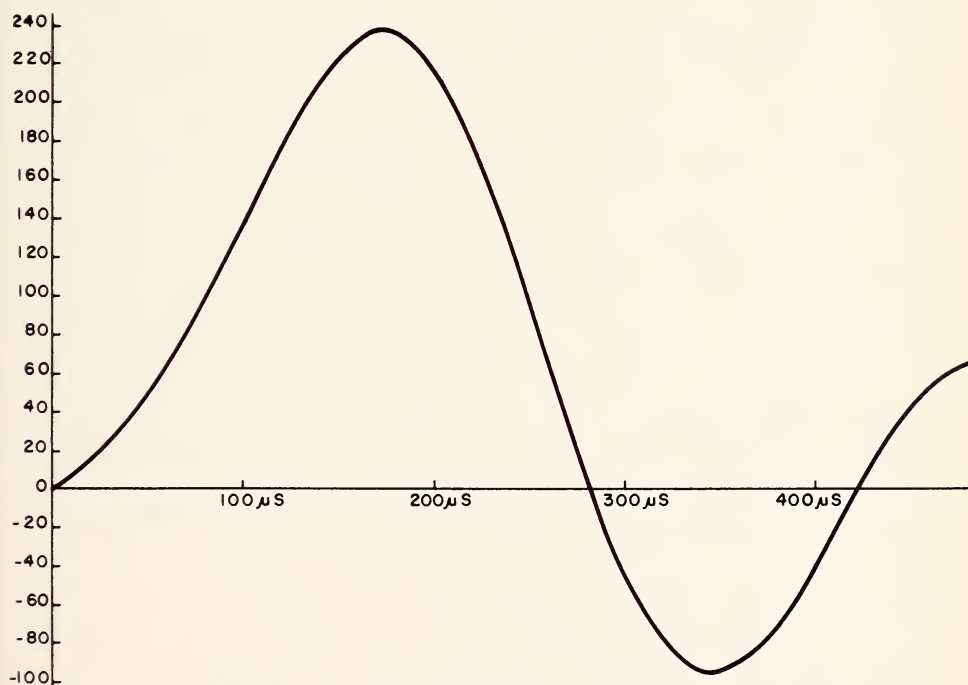


Fig. 3 — Impulse response of experimental channel

wavelengths. It seems clear that the bat must use some complicated and sophisticated form of signal processing.

4. Measure of Resolution.

Although there is fair agreement as to the qualitative meaning of resolution i.e. the ability to locate and distinguish targets close together, it is another matter to be definitive and quantitative about this concept. The problem has been approached in many ways and it is fortunate - one could hardly say fortuitous - that the resulting predictions have a fair amount of agreement. They also agree with the rather intuitive approach that the resolution should be of the order of the beam width. Of course just like bandwidth, beamwidth as will be seen from figure 2 has any value depending on the level below the centre response at which the width is measured but the generally accepted measure unless otherwise stated is the width between half power points.

As stated earlier there is Fourier transform relationship between the aperture distribution and the far field angular spectrum. There is thus an analogue which can be drawn to that other well known transform pair - a function of time and its spectrum. Care has to be taken in carrying this analogy too far because in the aperture case both functions are in general complex whereas functions of time are

real with the concomitant spectrum containing pairs of frequencies which are complex conjugates.

Using this analogy Welsby applied sampling theory to show that if the far field angular spectrum is completely unknown then even in the absence of noise there is a limit to the fineness of detail which one can resolve and that this limit is fixed by the number of half wavelengths contained in the aperture. However if some knowledge is available about the far field spectrum e.g. targets are spaced fairly widely apart and can be considered as point sources then it is possible that this knowledge can be exploited to enhance the resolution.

In considering the restrictions imposed by the relationship between the far field and the aperture distribution it is convenient to restrict the discussion to a line aperture in order to make the diagrams and mathematics simpler. There is no difficulty in extending the results to the plane aperture. The Fourier transform pair for this case is:-

$$Q(s) = \int_{-\infty}^{+\infty} P(x) e^{-j2\pi s x} dx \quad \dots(1)$$

$$P(x) = \int_{-1}^{+1} Q(s) e^{j2\pi s x} ds.$$

$Q(s)$ = far field angular spectrum

$P(x)$ = aperture Distribution

where s = $\sin \theta$

x = y/λ

θ = far field angle

y = distance along the line aperture.

It will be noticed that the far field function $Q(s)$ is in terms of the variable $\sin \theta$ so that for real angles $s \leq 1$. Remembering the analogy of the relation between the spectrum and the time waveform it will be seen that if s is less than unity then $P(x)$ can contain no frequencies greater than this. The sampling theorem states that a function containing no frequencies greater than W can be represented by samples taken at a spacing of $\frac{1}{2W}$ and it would appear that it is necessary to define the aperture function at spacing of x of only $\frac{1}{2}$ i.e. spacing of $\lambda/2$ along the actual aperture. This of course would be true if the function $P(x)$ contained a very large number of samples - in theory an infinite number - but in practice, as we have seen, the aperture is normally only a small number of wavelengths long. This truncation causes a smearing of the measured angular spectrum.

In fact what we measure is

$$Q'(s) = D(s) * Q(s) \quad \dots(2)$$

i.e. the convolution of $D(s)$ the directivity function of the array with the actual spectrum $Q(s)$. It would appear from this argument that the resolution properties of the array are limited in spite of the absence of noise but while in practice the resolution is in general limited to the beamwidth, in theory this is not so.

The problem has close relationship to a similar problem in communications. In communication systems the transmitter is modulated with an intelligence which we wish to convey to the receiver despite the effects of the intervening corrupting channel. On the other hand in Radar and Sonar systems the transmitter is modulated in order that we can determine at the receiver the corruption imposed by the channel; it is this very corruption which constitutes the information that is required. Shannon showed that information could be transmitted by a channel of bandwidth W at a rate of

$$W \log_2 (1 + S/N) \text{ bits/sec} \quad \dots(3)$$

and hence although the channel bandwidth may be limited if there is no noise the communication rate should in theory tend to infinity.

In spite of this, statements are still made saying that the communication rate is limited in a band limited noiseless channel⁽¹⁵⁾. The fallacy lies in the method of detection. As was shown by Hartley⁽¹⁶⁾ the rate

of transmission is limited in a system in which the decisions are based on single samples of the output waveform, since when the impulse response of the channel causes the higher rate pulses to run into one another mistakes will occur. However if the impulse response is known and measurements are made over a large number of points before a decision is taken, it is possible in theory to determine the transmitted waveform, no matter how fast pulses are transmitted. Hacking⁽¹⁷⁾ programmed such a problem onto a computer and the results were as predicted. He took a typical 4 kc/s low pass filter with an impulse response as shown in Figure 3. This he represented by a series of coordinates and so was able to stimulate it on a digital computer. The output from the channel is simply the convolution of the input time waveform with the impulse response

viz:-

$$f_o(t) = \int f_1(t) h(t - t) dt. \quad \dots(4)$$

where

$$\begin{aligned} f_o(t) &= \text{Output waveform} \\ f_1(t) &= \text{Input waveform} \\ h(t) &= \text{Impulse response.} \end{aligned}$$

From the output waveform and a knowledge of the impulse response it was possible to predict the corresponding input waveform. Figure 4 shows a typical case for an input data rate greater than twice the bandwidth. It can be seen that single point decisions will be in

error on a number of occasions whereas the computer made no errors in decoding at this rate.

Returning to aperture functions, and considering the truncated aperture distribution $P(x)$ then in theory if this waveform is known exactly it should be possible to measure all its derivatives and hence use Taylor's theorem to predict the values outside the truncated region. In reference 18, Ksienski states that one may obtain practically any desired amount of information (subject to noise level) regarding any object, by sampling an aperture of a fixed size or sampling the output of that aperture as a function of scan angle. The more information desired the larger the number of required samples and the more involved and precise the operations must be. But in principle, there is no theoretical limit.

Schelkunoff⁽¹⁹⁾ showed that the directivity function of an array may be expressed as a polynomial and that if there were n elements in the array the polynomial has $(n - 1)$ factors. Thus there will be no more than $n - 1$ zeros in the range of real angles provided the n elements are not spaced at greater than half a wavelength apart. The position of these $n - 1$ zeros can be placed at will in the directivity function and thus it should be possible to resolve $(n - 1)$ targets by removing the zeros one at a time or having $(n - 1)$ outputs

each one corresponding to the direction of one of the zeros.

5. The Ambiguity Function.

The criterion of separability which Woodward used is similar to the mean square error criterion, i.e. a measure of difference between two waveforms $S_1(t)$ and $S_2(t)$ can be defined by the expression,

$$\mathcal{E}^2(\tau) = \int (S_1(t) - S_2(t))^2 dt \quad \dots(5)$$

If we transmit a signal $S(t)$ then the received signals from two small targets will be $S(t - t_0)$ and $S(t - t_0 - \tau)$ where $\frac{t_0}{2c}$ is the range of target 1 and $\frac{t_0 + \tau}{2c}$ is the range of target 2; c , being the velocity of the wave in the medium. It is required to find the minimum value of τ that still enables the targets to be distinguished from one another. Using the definition of equation 5

$$\mathcal{E}^2(\tau) = \int (S(t - t_0) - S(t - t_0 - \tau))^2 dt \quad \dots(6)$$

$$\mathcal{E}^2(\tau) = \int (S(t - t_0))^2 dt + \int (S(t - t_0 - \tau))^2 dt.$$

$$- 2 \int S(t - t_0) S(t - t_0 - \tau) dt \quad \dots(7)$$

The first two integrals represent the total energy returned from the targets so the resolution properties are determined by the final

integral. If we define

$$I(\tau) = 2 \int S(t - t_0) S(t - t_0 - \tau) dt \quad \dots(8)$$

then we wish $I(\tau)$ to be zero everywhere except where $\tau = 0$. The transmitted signal can be represented by a modulated carrier viz:-

$$S(t) = A(t) \cos \omega_0 t \quad \dots(9)$$

$$\text{Thus } I(\tau) = 2 \int A(t - t_0) \cdot \cos \omega_0(t - t_0) \cdot$$

$$A(t - t_0 - \tau) \cdot \cos \omega_0(t - t_0 - \tau), dt. \quad \dots(10)$$

The value of t_0 will obviously not affect the integral.

Hence

$$I(\tau) = \int A(t) \cdot A(t - \tau) \cdot \cos \omega_0 \tau \cdot dt \quad \dots(11)$$

This is known as the ambiguity function.

Usually the sonar or radar removes the phase information from the received signal and so only the magnitude of the expression (11) will be considered i.e.

$$I_A(\tau) = \int A(t) A(t - \tau) dt \quad \dots(12)$$

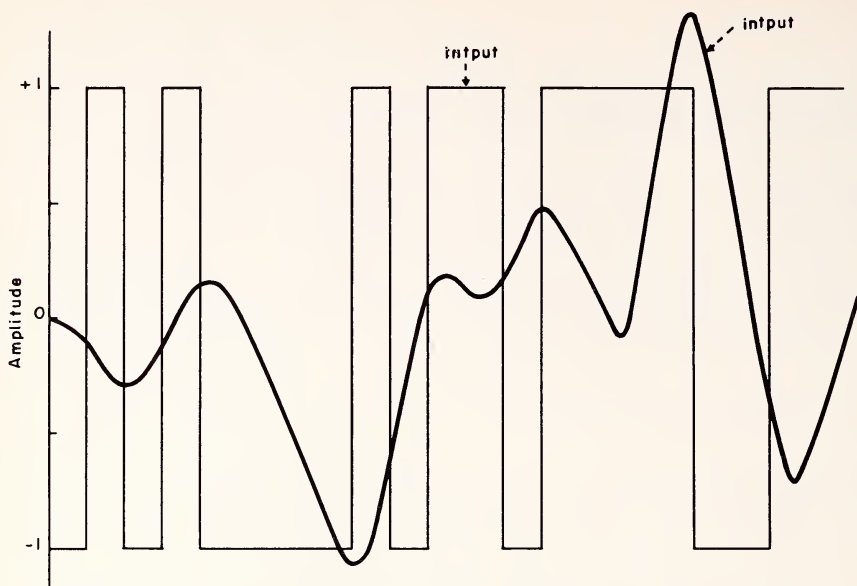


Fig. 4 — Typical input for a transmission rate of 12.5 bit./msec.

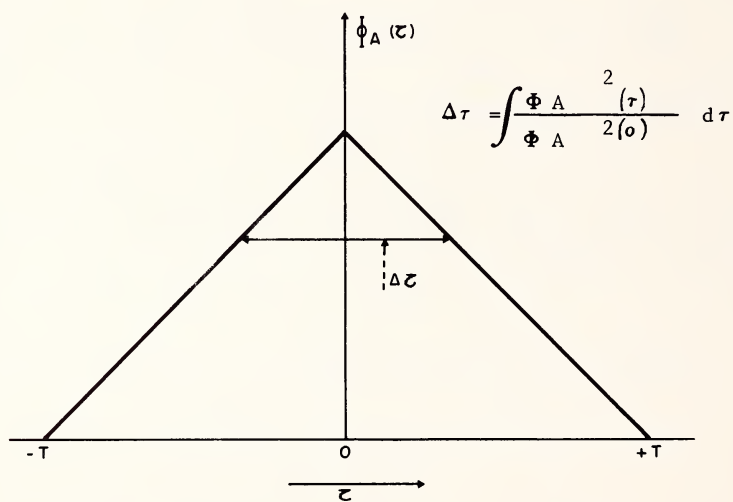


Fig. 5 — The ambiguity function for a single transmitted pulse

It will be seen that $\Phi(\tau)$ and $\Phi_A(\tau)$ are the autocorrelation functions of the signal and signal envelope respectively. For a single frequency pulsed sonar

$$A(t) = + A_0 \text{ for } -\frac{\pi}{2} \leq t \leq +\frac{\pi}{2}$$

$$= 0 \text{ elsewhere}$$

$\Phi_A(\tau)$ is shown for this case in figure 5. The autocorrelation of a function can often be found more easily by using the Weiner-Kintchine relationship i.e. using the fact the autocorrelation function and the power spectrum of a wave are a Fourier transform pair. For instance, in the example above, the amplitude spectrum is a $\frac{\sin x}{x}$ curve and hence the power spectrum will be a $\frac{\sin^2 x}{x^2}$ curve. The transform of this is the triangular wave shown in figure 5.

The time resolution is obviously related to the 'width' of the ambiguity function but as in the case of beamwidth many answers can be obtained simply by choosing an appropriate level at which to measure the width. However, a definition which has some useful properties is

$$\Delta\tau = \int \frac{\Phi_A^2(\tau)}{\Phi_A^2(0)} \cdot d\tau \quad \dots(13)$$

For the ambiguity function of figure 5 the resolution constant is $2T/3$. If one of the signals differs in frequency from the other due to the Doppler effect then the ambiguity function is a function of both range difference and doppler frequency difference viz:-

$$\Phi_A(\tau, f_D) = \int_{-\infty}^{+\infty} A(t) A(t - \tau) \cos w_d t \, dt \quad \dots(14)$$

If this expression is normalised to make

$$\Phi_A(0, 0) = 1$$

then it can be shown that

$$\iint \Phi_A^2(\tau, f_D) \, d\tau \, df_D = 1 \quad \dots(15)$$

i.e., the volume under the square of the ambiguity function is constant and is not dependent on the actual function. There is thus a 'trade off' relation between range resolution and doppler resolution. A short pulse gives good range resolution but poor doppler resolution, and a long pulse poor range resolution but good doppler resolution.

It is not the short pulse which is important but the frequency bandwidth covered by the transmitted signal. In pulse compression systems⁽²¹⁾ where a long frequency modulated pulse is transmitted the range resolution is determined by the frequency sweep and not by the pulse duration.

If the pulses transmitted are made periodic the doppler resolution is improved since the total time for measurement of the doppler is increased. The cost is an increase in the total width of range ambiguity function but by the production of a series of 'bumps' The received waveform at any instant might be due to an echo from a target at one of a number of ranges depending on which transmitted pulse caused the echo. However, due to the **fairly** severe attenuation of the transmitted wave with range the longer range targets are hardly likely to be mistaken for the shorter range returns. Thus there is an effective increase in resolution from the use of periodic pulses.

6. Application of the Ambiguity Function Concept to Angular Resolution.

Urkowitz⁽²²⁾ extended Woodward's analysis to the problem of the angular resolution of Radar systems and developed expressions for the combined ambiguity diagrams. One of the most interesting of his conclusions suggests that while frequency bandwidth improves range resolution it has no effect on angle resolution. This seems to be in contrast to the published results of other workers in this field^(23, 24, 25) who suggest that there is a frequency/space

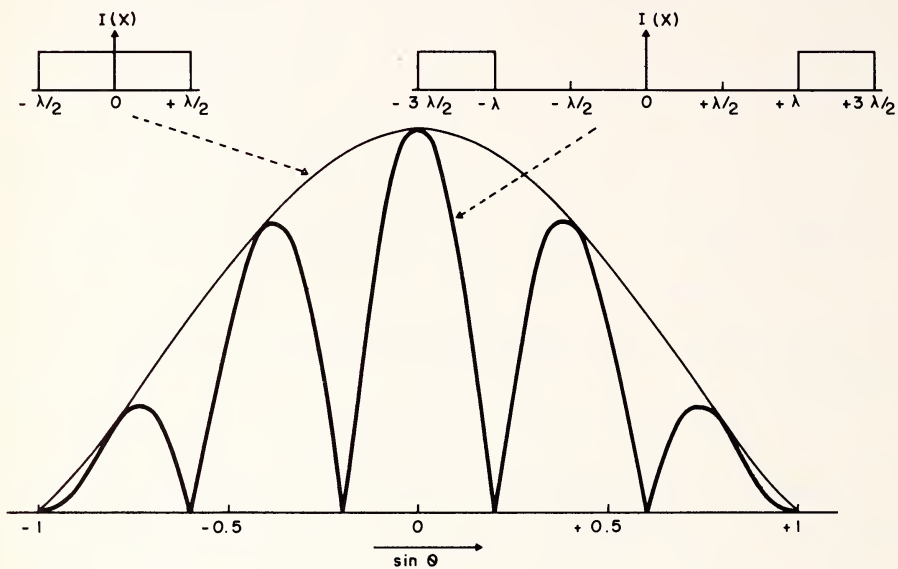


Fig. 6 — Directivity functions for two aperture illumination functions

equivalence for an array i.e. the number of space or array samples can be reduced if they are replaced by an equivalent number of frequency samples.

Urkowitz's ambiguity function for angle is dependent only on the effective length of the aperture in terms of the wavelength. The effective length of the aperture is defined by the expression

$$\frac{1}{L} = \frac{\int |I(x)|^4 dx}{\left[\int |I(x)|^2 dx \right]^2} \quad \dots (16)$$

where $I(x)$ is the illumination function. L can be seen to equal the actual length of the array for a uniformly illuminated aperture.

The resolution is defined as

$$\theta = \frac{\lambda}{L} \quad \dots (17)$$

It is interesting to note that the effective length is invariant to the spacing of the parts of the transducer. Say for instance we divide a transducer in half and separate these halves by some distance; since by equation 16 the effective length is unaltered then the resolution is also unaltered.

The directivity functions for two typical cases are shown in figure 6, an aperture of length λ uniformly illuminated and

two apertures of length $\lambda/2$ separated by $5\lambda/2$. Integrated over the whole range of angles it is no doubt possible that there is the same area under the square of the autocorrelation of these curves, but the ability to resolve using the different arrays must surely be different. If means can be found to remove the ambiguities then the resolution over a small range of angles is improved considerably. This is the principle used by Ryles interferometer⁽²⁶⁾ the ambiguities in this instance being unimportant as he was dealing with relatively isolated sources. As we have seen the same sort of ambiguity diagram results from repetitive range pulses since the system cannot distinguish in time of arrival between targets at ranges of R and $R + \frac{nTc}{2}$, where n is any integer. However these ambiguities are resolved in practice by the much reduced amplitude of the echoes from targets at these longer ranges. In the bearing problem if the transmission could be coded so that targets in different directions sent different signals then it should be possible to remove these ambiguities in the diagram and improve the resolution. Sending different frequencies in different directions seems an obvious method of coding⁽²⁷⁾ but this must be combined with a relatively narrow beam width on transmission. However, in theory this should present no difficulty since one can obtain any beam shape with a given aperture

by the techniques of super directivity^(28, 29); on the other hand experience has shown that these arrays are very difficult to achieve practically. It is interesting to note that if this technique is used the bearing resolution is equivalent to doppler resolution for the case considered by Urkowitz and one might expect a trade off between range resolution and bearing resolution in such a system.

7. Conclusions.

It is concluded from the foregoing arguments that animals using sonar for navigation do not form images in the optical sense but obtain the detailed information of their surroundings from a sophisticated signal processing technique. It is further argued that although the dimension of their arrays in terms of wavelength is fairly limited this does not necessarily limit the resolution since provided the signal to noise ratio is large then there is no theoretical limit to the resolution obtainable.

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SUMMARY

The limitations and controlling factors in the performance of a generalised sonar system are discussed. The possibility of forming acoustic images analogous to optical images is examined and it is shown that although equipment can be built using such techniques, it is unlikely that animals which navigate by sonar use this method because of the smallness of their apertures in terms of wavelengths. However, the alternative approach of signal processing by scanning is shown to be equivalent and with good signal/noise ratios to be capable of high information rates.

A quantitative method of measuring resolution is discussed and shown to lead to some interesting conclusions.

DISCUSSION

by

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Dr. Batteau and Dr. Griffiths have dealt with sonar theory in a very general way. As a biologist I should like to add some more specific ideas suggested by analysing the various signals of bats. These depend largely on a simple feeling of admiration for and confidence in the results of evolutionary development. They do, however, lead to a degree of caution in arguing about possible mechanisms in animal sonar from the consideration of man-made systems.

For instance, it is natural to assume that animals operate on polar co-ordinates, with 'fixes' determined in range and bearing (even 'azimuth' and 'elevation', although hyperbolic surfaces are probably involved), but possibly this is not always so. We still know very little about the sort of information an animal actually needs. The very term 'echolocation' might be misleading since the information obtained is almost certainly not always of a positional nature. Concepts taken from human systems inevitably form the initial working hypotheses, but they must be applied carefully to the needs of other species which are very varied.

It is clear that passive hearing, in its normal role of receiving and decoding acoustic communication signals, is concerned with some aspect of sound analysis. In echolocation however, only changes in the sounds, imposed by the environment, are informative; the pulse structure is already defined at the time of emission. But one would not expect an animal to subjugate all its 'normal' responses to the development of a sonar ability and thus a double system of information processing is likely. This may well confuse the issue when hearing mechanisms are examined experimentally.

Now sense organs can only communicate with the brain by means of nerve impulse codes in a large number of discrete channels, the nerve fibres. Each impulse lasts about 1 ms - longer than many of the acoustic pulses used for orientation. Each fibre conducts a maximum of a few hundred impulses per second at a velocity less than a quarter that of sound in air or one/eighteenth of sound in water. Although the information capacity of an acoustic nerve is difficult to assess, it would seem likely that some form of selection is performed before the neural level in order to reduce redundancy.

In recent years it has been found that many sense organs extract the relevant information at a peripheral level and transmit only this to the

afferent nerve. When a bat hunts for insects among foliage for instance, it is difficult to believe that this is not happening. For the analysis of such complex reflections it would seem both unnecessary and unwise to rely entirely upon a complete neural representation of the echoes. In fact it appears from the pulse structures that much of the information is contained in the fine structure of the waveform and there is no evidence that neural codes can represent high frequency sounds with this degree of precision.

The structure of bat pulses, however, suggests some simple physical means by which the essential information of their echoes can be extracted while other characteristics are rejected. Somewhat surprisingly there is evidence that these hypothetical transformations could actually be accomplished by a mammalian ear at a peripheral level, since the human ear is capable of very similar actions. The fact that many such psychophysical phenomena have not yet received a rigorous physical or physiological explanation does not invalidate them as a basis for argument. They are undoubtedly real although they indicate some unexpected properties of the ear. Since they would offer considerable advantages in sonar operation it seems natural to wonder whether they do play any part. Unfortunately they do not suggest any simple behavioural tests, and they would be difficult to investigate by electrophysiological sampling techniques. Most if not all the known neural responses (7, 9, 26-29) would be appropriate to such systems and these responses must be rapid because revised data are available every 5 ms at the higher pulse repetition rates.

Finally, nature is notably flexible and sophisticated. It seems unlikely that any readily available source of information will be rejected by an animal, even if it only confirms the results obtained by other means. We should not assume that there is a single mechanism used by all species,

or even that any one species is restricted to a single mechanism at a time. Any speculation should therefore bear in mind all the known characteristics of the systems, especially their differences, even if these are not yet explicable. Besides pulse structure, such characteristics include oral or nose-leaf emission, monaural or binaural reception, movements of the pinnae and aural anatomy (19).

The various bat pulses, as outlined earlier (22), show two well defined frequency patterns - downward sweeps (f.m.) and periods of constant frequency. Although these may be combined consecutively in the same pulse, their sonar properties are quite distinct and they are best considered separately.

Wide bandwidth pulses

The frequency-sweep pulse is typically short (0.5-4.0 ms), but has much wider bandwidth than a pulse of similar shape with a constant carrier frequency. It therefore possesses the advantages of chirp radar (13) by an increased 'mean-power x bandwidth' product for a limited peak-power. That the envelope shape contributes a minor part of the bandwidth is shown by the formulae of Klauder et al:

If ΔR = possible resolution in range

c = velocity of propagation (= 33 cm./ms)

t = pulse duration, τ = echo delay

Δf_s = extent of frequency sweep of transmitted signal,

then for a constant carrier frequency, and a square or a $\frac{\sin x}{x}$ shape, with $t = 1-4$ ms.:

$$\Delta R = \frac{ct}{2} = 16.5 \text{ cm.} - 66.0 \text{ cm.}$$

while for frequency sweeps, where $\Delta f_s = 50 \text{ kHz} - 12.5 \text{ kHz}$:

$$\Delta R = \frac{c}{2 \cdot \Delta f} = 0.33 \text{ cm.} - 1.32 \text{ cm.} - \text{an improvement}$$

factor of 50. Even a sweep of 5 kHz is as 'effective' as a constant-frequency pulse of only 0.2 ms. duration.

But contrary to what has been supposed (25, 1) it is not necessary to invoke Klauder's pulse-compression mechanism to realise these advantages. The information produced by this type of pulse can be retrieved in other ways, just as there are ways of producing a frequency sweep other than by passing a short pulse through a pulse-expansion network. The advantages lie in the pulse itself and not in a particular type of receiver. Klauder et al appear to claim that improved signal/noise is achieved only by the larger mean-power radiated, and this is to be expected since neither bandwidth nor energy of the echo is changed by compression. A pulse compression system seems unlikely in bats, since there is no evidence for a physical delay-equaliser in the ear (1), while at the neural level multiple echoes would compete in a situation of impulse congestion.

In effect pulse-compression preserves the temporal nature of τ so that it is suitable for, say, a PPI display. An alternative mechanism, which transforms τ completely, is to measure the difference in frequency f_b between signal and echo.

$$\text{Then } f_b = \tau \cdot \frac{\Delta f_s}{T}$$

This autocorrelation-like process utilises the full bandwidth, reduces the information to a non-redundant form, requires only a frequency analyser (the cochlea) for its interpretation and reduces problems of masking to permit the appreciation of a complex environment. It would be sensitive enough for differences in f_b at the two ears to give directional information, and f.m. bats appear to rely heavily on binaural interaction. Directional ambiguities will be reduced rapidly in practice by successive observations during movement.

This system is of course based on polar co-ordinates. It places the main onus for time-keeping on the rate of the frequency sweep, although the control of this is not yet understood and its stability cannot be assessed. The same principle is used by f.m. radio-altimeters, although there the relatively low beat-frequencies are often limited to values that are coherent throughout a train of pulses.

When this mechanism was first conceived (20, 21) it was thought necessary for f_b to be detected as a physical beat-note by a multiplicative process before the cochlea could respond to it. But then the objection was made (4) that some bats shorten their pulses as the range is reduced so that temporal overlap never occurs at the ear and a beat-note cannot be produced. However, Fourcin (5) and Wilson (this symposium) have recently shown that when a signal is added to the same signal after a delay τ , the response of the human ear shows a series of spectral maxima spaced apart by integral multiples of $\frac{1}{\tau}$. This periodic pattern is of course shown by the Fourier spectrum analysis, but its detection by the ear is somewhat surprising, for it implies that phase information can be physically retained within the ear. Of particular interest is an experiment in which a noise-signal in the band 1-3 kHz is presented to one ear together with its time-delayed 'echo'. The peaks in frequency distribution are clearly heard as a tone-like sensation of $f = \frac{1}{\tau}$. The sensation is, however, not subject to the same masking as a pure tone stimulus of similar frequency and 'loudness'.

A similar result has already been applied to bats by Nordmark (15), although the influence of bandwidth and the internal structure of the pulse was not taken into account. Now in the case of a frequency-sweep signal, the pattern of Fourier maxima will be sequentially scanned by the

echo, which will therefore be effectively amplitude modulated.

$$\text{Scan-rate} = \frac{\text{sweep-rate}}{\text{peak separation}} = \tau \cdot \frac{\Delta f_s}{t} = f_b$$

Thus maxima will be encountered at a rate equal to the rate of beating during overlap, but of course there is no limitation to the condition of overlap itself. In other words, autocorrelation mechanisms for determining

τ are limited by the time for which phase information can be retained and not to $\tau < t$. Fourcin has shown that this time is at least 10-15 ms. in the human cochlea for noise signals of 1-3 kHz.

Since neurons are only called upon to measure the spectral peak-spacings, or the frequency at which they are scanned by a sweep, there would appear to be no signal-frequency limit beyond the physical responses of the middle-ear and cochlea. If such a mechanism can work at high frequencies, the elimination of overlap by some bats would now suggest that actual beats are undesirable. They would, for instance, degrade the effective power-spectrum of the pulse. One frequency of the echo is 'matched' to a different frequency of the original pulse to produce a beat, but to the same frequency by phase-retention mechanisms. Even the examples of 'controlled overlap' found in Chilonycterine bats by Novick (16, 17, 18) fall into this category for the transmitted sweep only overlaps with a constant-frequency part of the echo and apparently not with the echo-sweep.

It is interesting that Hanbury Brown and Twiss (10) have shown that the diameter of a noise-source can be measured by an interferometer in which correlation is preceded by signal-amplitude detection, with consequent loss of phase. Whether this technique could be used after transmission by neural codes, with sweep signals and using a narrow base-line, is not obvious. But such methods would be worth considering for binaural effects where phase information is also lost. For instance, binaural correlations

at a neural level, postulated by Kaiser and David (12) for improving signal detection, might be reversed to yield directional information.

Further information can be obtained from a frequency-swept pulse by analysis of its echo-spectrum. This is not only modified by the reflecting properties of the target, but also by the directional properties of both emitter and receiver. The directional properties of the ears of f.m. bats, as a function of frequency, have been directly examined by Grinnell and Grinnell (8), who have convincingly shown how bearing might be measured in this way by two ears. Similar considerations must also apply, to some extent at least, to the oral emission of pulses, but a much more interesting case is offered by nose-leaf emission in the f.m. *Phyllostomatids*. As argued elsewhere (22), each harmonic component must produce a different radiation pattern and each pattern will change as the frequency falls. Thus a great deal of directional information could be obtained from a spectral analysis of the echo throughout its sweep. An analogy might be drawn with phase-scanning from an array of transmitters, although in a nose-leaf the phase difference is always zero and the frequency is changed.

Finally the presence of a more complex harmonic signal-spectrum may serve to increase the bandwidth without increasing the pulse duration or the extent of the fundamental sweep. This inevitably reduces the power at any frequency, since in effect different parts of the sweep are being transmitted simultaneously; it may be significant that this type of pulse is generally restricted to low intensity bats, such as *Phyllostomatids*, while the loudest species like *Vespertilionids* often suppress harmonics

to a marked extent. Otherwise this feature only appears to affect the foregoing theoretical arguments by an increased contribution to bandwidth from the rise and fall times.

The effect of Doppler shift on all these mechanisms is small. Indeed, Cahlander has calculated (3) that pulses of this type can contain little velocity information. Relative velocity can only be measured by successive discrete measurements of range, using several pulses.

Narrow bandwidth pulses

More puzzling than the f.m. pulses are those of extremely constant frequency which may be relatively long in duration (up to 100 ms). The terminal frequency sweeps of many such pulses can be ignored here since they occupy only a small fraction of the pulse and can be considered separately. Then the slow rise and fall times (as long as 2-5 ms) give extremely low bandwidth values; the autocorrelation function must be broad and oscillatory with a period $\frac{1}{f_s}$. Yet although the measurement of range is evidently not possible, these emissions do appear to be useful for, when present, they represent a large proportion of the total pulse energy.

The fact that pulses of this type inevitably overlap at the receiver with echoes from all reasonable ranges suggests that Doppler frequency-shift could easily be measured by a beat-frequency mechanism. This is very sensitive at the signal-frequencies used:

If, $f_s = 100$ kHz and $v =$ relative velocity $= 10$ m/s,

$$\text{then } f_b = f_s \cdot \frac{2v}{c + v} = 6 \text{ kHz}$$

Doppler shift could also be detected by a spectral-peak-spacing pattern, the whole of which would now be 'scanned' (by contraction or

expansion with changes in range) while the echo-frequency remains constant. The behaviour of this mechanism is again identical to that of f_b and also to that of standing-wave patterns between transmitter and target. But due to overlap, the necessary phase information is retained in the signal itself and there is no need to postulate a phase memory.

Although comparison of phase differences of the beat-frequency at the two ears could give binaural bearing information, this is unlikely at higher f_b , and Møhrres (14) has reported that Rhinolophus at least is little hampered by monaural operation. However, these animals are markedly dependent upon rapid ear movements which appear to scan the environment. While the directional properties of the pinnae would not seem to be pronounced, their movement will subject the incoming echoes to further Doppler shifts and analysis of these could improve the inherent directionality. That such shifts can be significant was indicated by the use of an acoustic Doppler method (23, 21) to confirm the synchrony of ear movement and pulse production (6). It is also worth pointing out that the nostril spacing of $\frac{\lambda_s}{2}$ gives a constant radiation pattern that can also provide some bearing information if scanned by movements of the head or nose-leaf. This relation, first noticed by Møhrres, has been found to hold good for several Rhinolophids and Hipposiderids with signal frequencies from 40 kHz to 150 kHz.

It is, however, possible to obtain range information from a constant-frequency signal if certain assumptions are made. A small target produces an echo-intensity proportional to R^{-4} , which is a non-linear function falling to 1/16 (-12dB) each time the range doubles. Since the change-in-range

over a given period can be measured by integrating the relative velocity (i.e. by counting the Doppler-beat cycles since each cycle denotes a change-in-range of $\frac{\lambda_s}{2}$), it is possible after a short time to deduce the range remaining.

This is equivalent to measuring the intensity of echoes at two ranges, R_1 and R_2 , and solving for R_2 in the simultaneous equations for $(R_1 - R_2)$ and R_1/R_2 . The process is easier to visualise by the more realistic decibel scale which represents proportional changes in range. Thus a difference limen of 1dB would be able to register a change-in-range of 6% while 0.5dB would detect a change of only 3%.

It would be essential in this mode to exclude changes in intensity due to movements of the target within the directional sensitivity pattern of the ear. Here is yet another possible explanation for the ear movements - the environment might be deliberately scanned and the peak signal taken to represent the 'true' value of echo-intensity.

This mechanism does not apply directly to large surfaces since a plane specular surface gives an inverse square law (doubled range gives -6dB) and curved surfaces give other laws, but such cases could easily be detected, or even allowed for, on the basis of bearing information and total echo-intensity. At first sight this system appears paradoxical since it is feasible with a signal of zero bandwidth. But the system bandwidth must also include the Doppler shifted signal, and the smaller the shift the longer it takes, so that the 'bandwidth x time' laws hold good. Radar formulae also state that range resolution is a function of bandwidth, and with a zero bandwidth signal it would be quite impossible to discriminate

between two small targets with the same velocity relative to the receiver. Nevertheless, all the information that can be obtained from such a signal is preserved in the peripheral transformations proposed and could be of considerable use to an animal hunting flying insects. Rhinolophus, for instance, is said often to hang from a branch, waiting for passing insects which would contrast very sharply against the background. Similar information in fact seems to be used by humans for localising sound sources by passive hearing alone, where only an inverse square law applies. But is the attempt to convert velocity information to polar co-ordinates just a human fancy?

It is worth mentioning here that the cochleae of the Rhinolophoidea have a different form from those of many other bats and show several unique features (19), although these cannot yet be explained in physical terms. It is a pity that no neurophysiological studies of central responses have yet been made on this group.

Some species, such as Emballonurids, use shorter constant-frequency pulses (less than 10 ms) with little or no terminal sweep but with several harmonic components. These are somewhat puzzling since they do not appear to be ideal for Doppler sensing, and in the absence of a nose-leaf the slight effective broadening of bandwidth would seem to be of little value. Admittedly these bats are considered to be the most primitive in the taxonomic scale, but they are highly successful in tropical regions and their performance deserves more detailed study.

Two further problems may be mentioned in passing. The first is whether insectivorous bats can select their prey to some extent by measuring the rate of its wing-beats. This is easy with Doppler measurement and the method has been used in investigations on moths (in preparation). Roeder (24) has shown that the reflectivity of active insects varies greatly with the aspect of the wings so that echo-intensity can also be used. During pursuit manoeuvres f.m. bats emit pulses at up to 100-200 per second which would be sufficient to monitor the wing-beats of many insects (e.g. moths at 30-80 Hz) and to produce 'strobophonic' effects for faster ones.

The second problem concerns the rapid trains of ultrasonic pulses emitted by many moths when a bat is in pursuit (2). Although the function of this interaction is not yet clear, it appears to be protective for the moth. But different moths produce quite a variety of signals whose properties need to be defined. What, for instance, are the ideal properties of a sound used to mask a bat-pulse echo? Probably they will vary with the form of the signal to be countered so that acoustic physics might be a factor in complex ecological predator-prey relationships, the problems of which have as yet hardly been posed.

The general conclusion of this paper is that interference techniques are remarkably simple and elegant ways of handling signals. They appear so promising at various points in the sonar systems of bats that the bats might well have discovered this for themselves.

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SUMMARY

The ultrasonic orientation signals of bats are of two basic types and each produces information of a different kind. Useful information can be obtained by the analysis of phase, or frequency or intensity of the pulses of either type. Ways in which this might be done, within physiological limitations, are discussed in an attempt to reconcile physical and biological considerations.

Bats
 Neural coding
 Central Nervous system
 Bandwidth
 Frequency-sweep signals
 Constant frequency signals
 Interferometry
 Doppler shift.

X

Types et protocoles
d'expériences à effectuer
pour obtenir des résultats comparatifs

Experiments to conduct in order
to obtain comparative results



TYPES ET PROTOCOLES
D'EXPÉRIENCES A EFFECTUER
POUR OBTENIR
DES RÉSULTATS COMPARATIFS

par
Jean-Claude LEVY

INTRODUCTION

Dans l'introduction, je chercherai à situer le problème et à souligner le caractère "subjectif" de la perception chez l'animal. Les quelques faits cités à l'appui de la discussion ne le sont qu'à titre d'exemple, il importe peu qu'ils paraissent trop simplistes ou qu'ils n'aient pas tous fait l'objet de vérifications expérimentales rigoureuses.

Les expériences qui seront proposées dans la seconde partie de cet exposé pourront contribuer à éclairer ce qui pourrait sembler encore obscur à la lecture de l'introduction.

Dans le domaine qui nous intéresse, il y a une erreur à ne pas commettre : se représenter le fonctionnement des systèmes biologiques d'après celui des systèmes technologiques imaginés par l'homme.

La nature ignore la métrique et les données quantitatives : elle procède par "reconnaissance des formes" ; c'est-à-dire quand un système biologique tel que le cerveau d'un être supérieur reconnaît un signal, c'est qu'il connaît la réaction qui lui est appropriée.

La reconnaissance d'un signal se fait par superposition plus ou moins parfaite d'une configuration imposée de l'extérieur avec un certain nombre de "clichés", lesquels, dans le règne animal, correspondent à des structures réflexes innées ou à la mémoire basée sur le conditionnement : cette superposition est purement empirique, et l'analyse mathématique rigoureuse ne peut l'aborder que dans le cadre des généralités, chaque cas particulier ne pouvant pas se mettre en équation.

La correspondance entre un signal et une réponse appropriée constitue chez les êtres primitifs un phénomène réflexe relativement élémentaire.

Les êtres plus évolués, soit en tant qu'unité biologique, soit au travers de systèmes nerveux spécialisés, tiennent compte d'un grand nombre de données. Un même signal déclenchera, suivant les cas, plusieurs réactions différentes, et

ceci par suite d'un mécanisme beaucoup plus compliqué pouvant se résumer en trois points :

1. Réactions immédiates ou réflexes.
2. Recherche dans la mémoire d'un surcroît d'information.
3. Programme d'action tenant compte de la dite information.

Il s'agit toujours de comparaison ou de reconnaissance de formes, il n'y a jamais de mesure au sens propre du mot.

Donnons un exemple :

Un calculateur de tir a repéré un mobile à atteindre : il fera un certain nombre de mesures numériques (distance, position angulaire, vitesse, etc...) ; il en déduira la position "avion futur" dont les données seront numériquement transmises au pointage.

L'animal observe sa proie, il reconnaît dans son mouvement une certaine "configuration spatio-temporelle" qu'il rapprochera de celles qu'il a déjà connues, et dont il pourra prévoir la fin avant qu'elle ne se produise réellement : c'est ainsi qu'il déterminera la position de la "proie future", et ceci sans avoir fait aucun calcul.

Naturellement, en plus de la faculté d'extrapoler le mouvement qui vient d'être décrite, l'animal possède en plus celle de suivre d'une façon continue son objectif et de corriger son mouvement d'après ses observations. Mais il y a toujours une part d'extrapolation : la preuve en est qu'un mouvement imprévu de l'objectif peut dérouter le poursuivant.

L'homme lui-même n'agit pas autrement et sait ordinairement extrapoler un mouvement uniforme ou uniformément varié ou encore une trajectoire parabolique avec ou sans rebondissement : un bon joueur de tennis sait où attendre la balle, mais son jugement peut être faussé si la balle est "coupée".

Ceci dit, que fait un animal (dauphin ou chauve-souris) quand il repère un objet fixe ou mobile ?

D'abord, il cherche à identifier l'objet en question, et cela pour pouvoir choisir entre deux programmes possibles : Attaque, s'il s'agit d'une proie comestible, d'un ennemi à détruire, ou encore éventuellement d'un ami susceptible de donner la nourriture ou de prodiguer une manifestation amicale.

Fuite, s'il s'agit d'un ennemi dangereux ou simplement d'un obstacle à éviter.

Cela fait, l'animal tiendra compte de la position et des mouvements de l'objet comme il a été dit plus haut.

Supposons par exemple qu'il s'agisse d'un obstacle à éviter, pour simplifier les idées, supposons qu'il s'agisse d'un obstacle impossible à contourner, obligeant à l'arrêt.

Pour comprendre ce qui se passe dans le cerveau de l'animal, mettons nous dans celui d'un automobiliste.

Ce qu'il perçoit : l'arrière d'une voiture dont les dimensions angulaires lui donnent une estimation de la distance de l'obstacle, ceci parce qu'il connaît ses dimensions absolues ; la variation avec le temps des dimensions angulaires lui donne une estimation de sa vitesse de rapprochement ; il a alors tous les éléments nécessaires pour se décider à freiner.

S'il s'était mis en tête de calculer en fonction de la distance, de la vitesse relative de l'obstacle, du coefficient de frottement de ses garnitures de frein, etc... la force avec laquelle il doit appuyer sur la pédale, il aurait eu le temps de se tuer : il doit y avoir une association directe entre la perception de la croissance des dimensions apparentes de l'obstacle, et la pression sur la pédale de frein. Ce ne serait qu'en cas d'accident que le conducteur pourrait, en rappelant ses souvenirs, évaluer, à postériori, sa vitesse et la distance à laquelle il avait aperçu l'obstacle.

Il en est de même d'un animal muni d'un système SONAR : il perçoit une configuration qui est celle de son signal d'émission suivi d'un écho, un écho très proche de l'émission signifie alors : obligation de ralentir, et ceci avec d'autant plus d'intensité que, d'une émission à l'autre, l'intervalle émission-écho diminue plus rapidement.

La notion de distance est, pour l'animal, quelque chose de très abstrait ou du moins de subjectif, car il ne dispose certainement pas d'unité pour la mesurer. S'il se trouvait derrière un SONAR animal un cerveau humain avec tout son acquis scientifique, ce cerveau aurait une perception directe de la distance, mais ce n'est pas le cas.

Dans des cas plus compliqués, l'animal, recevant plusieurs échos, sera capable d'élaborer des programmes plus complexes visant à contourner un certain nombre d'obstacles pour atteindre son but par le plus court chemin : peut-être, au cours de cette opération, peut-il faire une synthèse de ses perceptions et en dégager la notion de distance de façon à se donner une représentation géométrique de l'espace dans lequel il évolue : il s'agit là déjà d'un travail de synthèse très avancé dans l'échelle des capacités des organismes supérieurs.

Nous autres, les hommes, nous effectuons cette opération couramment grâce à nos yeux, le Dauphin le fait grâce à son système SONAR, cette opération nous semble très élémentaire, quand nous pénétrons dans une pièce, nous en avons tout de suite repéré la disposition, mais l'insecte (que nous sommes pourtant encore loin de pouvoir imiter) est incapable d'une telle généralisation, il n'y a qu'à voir le mal que nous avons à chasser une guêpe par la fenêtre ouverte.

Quelques exemples seront peut-être encore utiles pour se donner une idée exacte du caractère subjectif de la perception.

Un individu à front bas évoque l'idée de bestialité, et ceci même pour qui ne sait pas que ce sont les lobes frontaux qui permettent le plein développement de la personnalité humaine.

Il en est de même de tous les traits de physionomie, ou jeux de physionomie, qu'ils correspondent à des traits de caractère, à des symptômes de maladie ou à des états émotionnels.

Un sifflet de locomotive de note aigue évoque l'idée d'une grande vitesse, et ceci même pour qui ignore tout de l'effet DOPPLER.

Enfin un dernier exemple montrera que dans le doute, c'est l'estimation subjective qui l'emporte sur l'appréciation quantitative : l'estimation de la distance nous est ordinairement donnée par les dimensions angulaires d'un objet dont nous connaissons par ailleurs les dimensions absolues ; le brouillard fait paraître les objets plus loin qu'ils ne sont réellement : ils nous paraissent alors plus grands parce que les dimensions angulaires étant les mêmes nous nous trompons alors sur les dimensions absolues.

Pour conclure ce préambule qui pouvait sembler un peu trop long, disons que malgré la présence de leurs systèmes SONARS les Dauphins et les Chauves-Souris n'ont probablement de la distance qu'une notion subjective, et que s'ils sont capables d'en avoir une idée comparable à la nôtre ce ne peut être que par suite d'opérations intellectuelles déjà très complexes.

Chez les hommes eux-mêmes, la "métrique" est le privilège de quelques intellectuels, et ne concerne encore que les sphères tout à fait supérieures de leur activité psychique, dans presque tous les cas nous agissons d'après des données subjectives comme le font les animaux.

RÔLE DE L'INFORMATION

La façon dont l'animal ou l'Homme au naturel traite l'information est une chose, la façon dont l'Homme la traite avec son esprit et son arsenal scientifique en est une autre, mais de toute façon, cette information doit exister dans les signaux reçus.

Dans tous les systèmes évolués, cette information est rapprochée de celle qui existe dans la mémoire ; il y a là possibilité de correction d'erreurs et d'opérations sémantiques. Si cette information est traitée par des systèmes biologiques composés de millions ou de milliards de cellules, elle peut théoriquement être traitée par des calculateurs électroniques et des cartes perforées : dans quelques cas simples, ce traitement doit pouvoir être réellement effectué.

Un premier point est alors à traiter : de quelles informations ont besoin les animaux ? Quelles informations l'Homme peut-il utiliser s'il cherche à imiter les SONARS animaux ?

La supériorité des systèmes SONARS animaux sur les SONARS de fabrication humaine repose surtout sur deux points :

- 1° Possibilité d'effectuer la synthèse d'un grand nombre de signaux pour se diriger parmi les obstacles.
- 2° Possibilité de détecter un objet dans un environnement produisant un brouillage intense du signal.

La première de ces possibilités repose sur la présence d'un nombre énorme de cellules et il semble douteux qu'elle puisse avant longtemps être réalisée artificiellement.

La seconde possibilité, par contre, relève du principe général de la reconnaissance des structures, elle pose un principe de traitement de l'information et il n'est pas interdit de penser que , sur ce point, l'étude des systèmes animaux puisse fournir aux techniciens des renseignements intéressants.

Dans le domaine de la bionique, c'est-à-dire en ce qui concerne la possibilité de réaliser des dispositifs techniques imités des systèmes biologiques, les signaux sonores présentent sur les signaux lumineux un grand avantage, parce qu'ils sont reçus sur un nombre plus faible de canaux, deux en principe, alors que les signaux lumineux le sont sur les milliers ou millions de cellules de la rétine.

L'oreille interne effectue l'analyse harmonique du signal et le distribue sur de nombreux canaux, mais ce nombre n'est pas forcément prohibitif en cas de réalisation technologique, de plus, d'autres procédés pourraient être imaginés.

Le problème qui se pose à nous, expérimentateurs, est le suivant : connaissant le signal, quelle information peut-on en tirer ? Quelle information en est-elle extraite par l'animal ?

1. Recherche de l'information

Il faut pour cela disposer d'échos, et pour qui dispose d'enregistrements de cris d'animaux, il peut y avoir possibilité de les réémettre dans le même milieu, et de recueillir les échos d'obstacles bien définis.

Il faut alors, par exemple, rechercher si par les moyens connus, il est possible de détecter un objet dans un bruit ambiant (Expériences de Griffin sur la Chauve-Souris).

Nous proposons une méthode qui présente l'avantage de ne pas nécessiter la présence d'animaux vivants, de plus, il est possible de simplifier les opérations, c'est-à-dire de se placer dans des cas simples sans tenir compte des "caprices" des animaux utilisés pour l'expérience.

L'opération peut se décomposer en trois parties :

a) Découpage du signal sur ruban de magnétophone, de façon à isoler les "clicks" d'écholocalisation, en leur conservant, bien entendu, leur cadence naturelle de répétition.

b) Production des échos dans un milieu analogue au milieu

naturel de l'animal, et enregistrement sur deux pistes synchronisées du signal d'émission et des échos.

c) Analyse des enregistrements par tous les moyens dont disposent les techniciens.

Une bonne méthode consisterait à superposer par un procédé optique différentes courbes d'enregistrement, lesquelles auraient pu auparavant subir quelques transformations telles que le filtrage ou la détection. Cette méthode est empirique, mais elle est plus proche des processus naturels. Cela se fait avec l'oeil de l'opérateur et le cerveau qui se trouve derrière, peut-être pourra-t-on par la suite effectuer cette opération automatiquement, peut-être conservera-t-on un opérateur humain, cela n'entre plus dans le cadre du présent exposé.

2. Traitement de l'information par l'animal

Parallèlement au traitement "artificiel" de l'information, il sera nécessaire de savoir comment l'animal reconnaît l'information contenue dans ses échos. Cela se fera de deux façons :

a) Mesure des performances.

b) Modifications des échos naturels et tentatives de faire reconnaître par l'animal ces échos modifiés, de façon à identifier ce qui supporte l'information dans ses échos naturels.

MESURE DES PERFORMANCES

Par "performances" nous entendons ici "précision" ou "pouvoir discriminateur". Nous allons donner quelques exemples à titre non limitatif.

1. Détection d'un objet de petites dimensions devant un obstacle

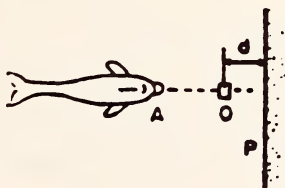


Figure 1

La fig. 1 indique la disposition : l'objet O se trouve à la distance d du plan P, l'animal (Dauphin ou Chauve-Souris) a les yeux masqués, il est lâché en A. On le dresse à toucher

l'objet qui pour commencer est placé à bonne distance du plan. Cela fait, on diminue d'un essai à l'autre la distance d jusqu'à ce que l'animal ne détecte plus l'objet.

2. Précision de la mesure de distance

Nous avons dit que l'animal ne savait pas ce que c'est qu'une distance, mais il reçoit quand même l'information correspondant à la distance et cette information peut agir sur son comportement ; peut-être même l'entraînement auquel il sera soumis pourra-t-il développer en lui la notion de distance.

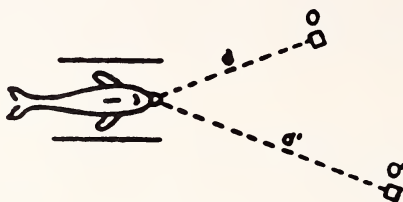


Figure 2

On place l'animal en A à l'entrée d'un carrefour en Y (fig. 2), en O et O' se trouvent deux objets, on dresse l'animal à toucher le plus rapproché, ceci en intervertissant souvent les côtés pour éviter que le sujet ne s'habitue à aller à droite ou à gauche. Selon un principe analogue à celui du cas précédent, on commence par un grand écart entre les distances d et d' , puis d'un essai à l'autre on diminue progressivement cet écart jusqu'à ce que l'animal ne parvienne plus à le déceler.

Remarque. Il faudra aussi tenir compte de la valeur absolue de d et d' car il est probable qu'à partir d'une certaine distance, l'animal ne se préoccupera plus des distances relatives d'objets qu'il estimera trop éloignés.

3. Evaluation de la vitesse radiale

On dresse l'animal à poursuivre une cible au moment où elle commence à s'éloigner ou à se rapprocher. On commence avec une vitesse notable que l'on diminue d'un essai à l'autre jusqu'à ce que le sujet ne réagisse plus.

Il sera intéressant de bien noter le début du mouvement et d'évaluer le temps qu'il faut à l'animal pour se décider à

attaquer : cela permettra peut-être de déterminer si l'application de l'effet DOPPLER lui permet de déceler le mouvement avec une seule impulsion (peu probable).

Si, comme il est naturel de le penser, il faut à l'animal plusieurs impulsions pour déceler le mouvement, ce nombre d'impulsions doit être en rapport avec la précision de l'évaluation des distances.

ECHOS ARTIFICIELS

Le problème revient à ceci :

- a) Tromper l'animal avec un écho artificiel lui faisant croire, là où il n'y a rien à la présence d'un objet fantôme.
- b) Modifier l'écho jusqu'à ce que l'animal ne se laisse plus tromper : les modifications qu'il aura fallu apporter à l'écho permettront de connaître ce qui, dans cet écho, caractérisait sa reconnaissance par l'animal, et quelles étaient les informations qu'il y recherchait.

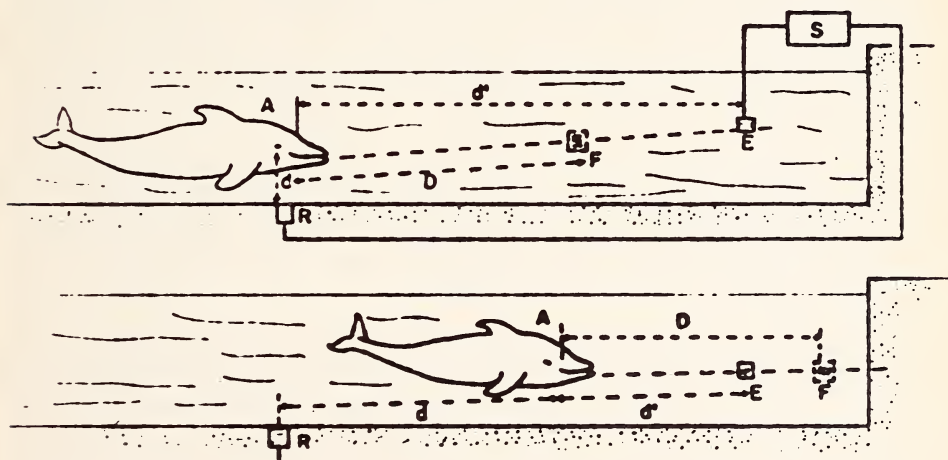


Figure 3

Le dispositif expérimental est représenté par la fig. 3.

En R se trouve un hydrophone récepteur qui transmet son signal à un hydrophone émetteur E. L'animal est en A à la distance d de R et à la distance d' de E. Le click d'écholocation est capté en R et réémis en E l'animal

croit alors détecter un objet en F sur la demi droite A E.
Cet objet se trouve à la distance apparente :

$$D = 1/2 (d + d').$$

Si l'hydrophone R peut être dissimulé près de l'animal (par exemple dans le fond du bassin, s'il s'agit d'un Dauphin) d est petit et l'on peut avoir :

$$D < d$$

Dans ces conditions le fantôme sera l'objet le plus proche détecté par l'animal.

Il est connu que le Dauphin émet un click d'écholocation dès qu'il a reçu l'écho du click précédent : sa fréquence d'émission permet donc de connaître la distance à laquelle il se trouve de l'objet le plus rapproché qu'il détecte, il sera donc possible de savoir si cet objet est le fantôme F ou l'hydrophone émetteur E.

Quand le dauphin s'approche de E il finit par s'éloigner de R, et l'écart $d - D$ diminue, s'annule puis devient négatif, c'est-à-dire qu'à partir de ce moment l'objet fictif ou réel le plus proche sera l'hydrophone E : de toute façon on verra l'animal se diriger vers E et seule l'écoute de ses clicks d'écholocation permettra de savoir s'il a, ou non, détecté le fantôme.

Si, ce qui n'est pas certain, l'animal "attaque" le fantôme, il aura l'impression que ce dernier s'enfuit en direction de l'hydrophone E, puis le dépasse, on ne sait pas alors si le Dauphin continuera à le poursuivre pour finir par le perdre, ou s'il s'en désintéressera.

En principe il est aveuglé, mais il peut être intéressant d'observer son comportement quand il détecte un objet qu'il ne voit pas, il est probable qu'il en sera très effrayé.

Entre les hydrophones R et E se trouve un système électronique S. Ce système comporte un amplificateur et des filtres permettant de modifier le signal pour "dénaturer" l'écho jusqu'à ce que l'animal cesse de reconnaître sa propre voix.

C'est ainsi que seront déterminées les caractéristiques de l'écho, bande de fréquence, intensité, enveloppe, telles que les utilise l'animal à la réception, ce qui peut différer des caractéristiques des clicks d'écholocation tels qu'ils peuvent être directement enregistrés.

C'est surtout l'étude des modifications du signal à la transmission et à la réflexion qui donnera les renseignements les plus intéressants sur la manière dont l'animal interprète ses échos.

Simulation de l'effet DOPPLER

Un double changement de fréquence permettra au système S de la fig. 3 de faire "glisser" toutes les fréquences composant le signal. Cela ne correspond pas exactement à l'effet DOPPLER théorique, car dans le cas présent le glissement est le même pour toutes les composantes, alors que la formule de l'effet DOPPLER est :

$$f/f = 2 v/V$$

- où f : est le glissement de fréquence,
 f : une fréquence composante du signal,
 v : la vitesse de rapprochement du but (comptée négativement si le but s'éloigne),
 V : la vitesse de propagation du son dans le milieu : air ou eau.

Mais comme les différentes composantes de fréquence constituant l'écho sont voisines, l'erreur ainsi introduite est négligeable.

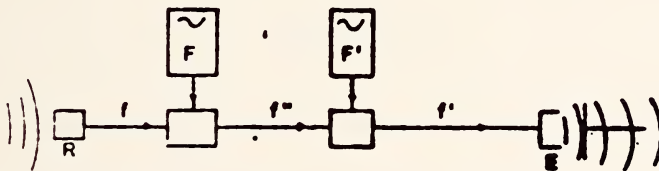


Figure 4

Le principe de l'opération est donné par la fig. 4.

On reçoit un click d'écholocation à la fréquence f .

Un premier changement de fréquence donne : $f'' = F - f$.

Un second changement donne : $f' = F' - f'' = f + F' - F = f + f$,
 en posant : $f = F' - F$.

Si l'animal se déplace, il pourra y avoir contradiction apparente entre la vitesse radiale du fantôme due au déplacement de l'animal, et celle qui résulterait de l'effet DOPPLER simulé : là encore, les résultats de l'expérience permettront de savoir dans quelle mesure l'animal peut déceler un effet DOPPLER.

CONCLUSION

Toutes les expériences dont le principe a été sommairement indiqué visent au même but : étudier les propriétés des "récepteurs" utilisés par l'animal, et leurs diverses possibilités de discrimination en fréquence, bande passante, variation de niveau, etc...

Parallèlement à ceci, des observations sur la façon dont se comporte l'animal dans des situations anormales pourront nous renseigner sur sa psychologie, mais cela nuira à la simplicité des opérations destinées à effectuer des estimations ou des mesures de ses performances.

Il faudra donc veiller à troubler l'animal le moins possible, et à lui faire paraître les objets vrais ou faux qui lui seront présentés le plus naturellement possible, c'est-à-dire de le leurrer le plus habilement que l'on puisse faire.

DISCUSSION

by

D. GRIFFIN

In planning this symposium we hoped that participants would not limit themselves to presenting new data but would establish sympathetic bridges between biological and physical scientists in the course of reviewing what is known about animal sonar systems. This was to be followed by a discussion of the most important next steps which ought to be taken. Dr. Levy has made a greater effort than most of us to achieve this second objective. I should therefore like to concentrate on the experiments he proposes in the second part of his paper in an effort to contribute my share to this vitally important bridging operation.

Obvious and elementary measurements for which a physicist asks are often extremely difficult to obtain from animals. The explanation may involve adaptations of natural sonar systems for particular patterns of behavior. The systems we have been considering are vastly more complex than we commonly appreciate, and it is a mistake to judge their nature and performance from our present limited knowledge. A bat, for instance, seems small and feeble compared to an airport radar with its heavy antenna rotating once every few seconds and its PPI screen that displays approaching aircraft. But we must recall that all the complex neurophysiological mechanisms discussed by Henson, Suga, and Grinnell are merely a small fraction of those that function in efficient coordination in less than one gram of bat brain. The complexity per gram (if I may speak in such imprecise terms) of a five gram bat is far more impressive than the airport radar. We must also avoid the related error of thinking of our instruments for analyzing animal sonar as more complex and intricate than the living mechanisms they help us to study. Oscilloscopes or even computers seem to me analagous to crude crowbars with which one might struggle to analyze the workings of a watch.

We should keep in mind the long evolutionary history of animal sonar systems. Bats were probably catching insects by sonar 50,000,000 years ago, and the natural selection assures the efficiency of these systems, for the animals' purposes not ours. If the performance falters, the animal starves; and this natural selection goes far to achieve reliable operation.

Performance measures should be related to the design objectives of the system. It would clearly be just as inappropriate to judge the performance of an insectivorous bat by asking at what distance it can detect a DC-8 as

to condemn the airport radar because it cannot fuel itself by catching insects. While the performance measures proposed by Levy are far closer to the mark than these farfetched examples, they are those of an engineer testing a sonar system.

To turn to Levy's specific proposals, the conference has demonstrated that several zoologists have been at work obtaining just the sort of information concerning animal sonar signals for which he calls. This has included, recently, the analysis of echoes determined at least approximately by calculation in the case of very simple shapes or by direct measurement for more nearly natural and hence more complex targets. We are often limited by the measuring apparatus available, especially by transducers.

If we had instruments with the sensitivity and signal-to-noise ratio of the animal's hearing, our analyses could easily be improved substantially. Only a few years ago the best microphones in existence would not detect the emitted orientation sounds of many bats. I was assured by acoustical engineers that these microphones, like the famous Western Electric 640AA, could not be improved upon. But in 1954 Kuhl et al developed much better microphones for high frequency airborne sounds, and analysis of bat sonar signals advanced within a very few years. Jamming experiments with bats could be much improved if better broad-band high frequency loudspeakers and appropriate power amplifiers became available. The obstacles to these improvements in measuring instruments are not merely financial, new engineering enterprise is needed to develop more refined measuring devices.

Most of the measurements of performance suggested in Levy's paper have been attempted, but it is entirely appropriate that he would call for renewed and greatly improved efforts in these directions. Let me explain why some of these measurements are more difficult than one might realize

and hence have not yet been carried out with satisfactory results.

I. Detection of an object close in front of a large surface. Earlier in the symposium we saw a motion picture film in which a porpoise appeared to be doing this, but the surface was smooth and reflection was largely specular. Hence the signal-to-noise ratio of the target echo was probably almost as high as though the target had been in open water. In Fig. 1, one would need screens or barriers to force the animal to approach perpendicular to the large surface, or a "matte" surface reflecting about equally over a wide angular range could be arranged. Bats land on small toe holds which must return echoes with very poor signal-to-noise ratio, and this should be studied quantitatively with appropriate controls for spatial memory.

As mentioned by Grinnell, we performed some quantitative experiments some years ago on bats' ability to avoid wires near the hard wall at the end of our ten meter flight room. With small wires half a meter from the end wall there was a clear increase in the threshold size of wires. Increasing the wire diameter could compensate for the interference from echoes of the end wall (Griffin, 1959).

II. & III. Training bats to make discriminations such as those suggested for distance and radial speed might be possible. But simple operant conditioning to sound in order to obtain absolute and differential thresholds has been surprisingly difficult. Dalland (1965) has recently obtained simple auditory thresholds at a few frequencies, but only after several months of work and only with a very few individual bats. With porpoises this type of experiment would probably proceed more rapidly. Yet bats can learn quite readily provided the behavioral situation is one which makes sense in their way of life, as in our discrimination experiments with disks and mealworms.

Concerning artificial echoes, I have tried many variants of the experiments proposed and only one of these gave even marginal responses from the bats (Griffin, 1958, pp. 192-193). Briefly we attempted to simulate insect echoes and cause bats to turn toward a high frequency loudspeaker. The loudspeaker was mounted on a long pole, and as the bats flew over our microphone their orientation sounds were rebroadcast from this speaker. If the bats judged distance by the time delay between emitted sound and returning echo, there should have been a phantom echo that appeared to arise in front of the pole. About one quarter of the bats did turn toward the pole and speaker although practically none did so with the speaker disconnected. But as soon as they passed over the microphone, the neat geometrical relationship sketched in Levy's Fig. 3 ceased to exist.

Except for this sort of insect pursuit behavior, it is difficult to arrange conditions where bats can be expected to behave differently because of a false echo and thus tell us by their changed behavior that they even detect the false echo let alone that a specific illusion is established. In all the practicable cases I can think of there is also a real echo from the loudspeaker itself, and on approaching the speaker the bat receives a phantom echo that gradually converges on the real echo. Hence avoidance or landing behavior will be difficult to distinguish from that based on real echoes. Training bats to react to false, artificial echoes may be possible and fruitful; we are preparing to attempt this in the near future.

My own suggestions for improvements in experiments on bat sonar are the following:

A. Locating a bat by differential arrival times of its orientation sounds at several microphones is often suggested as a way to improve our

recording of a moving bat's position during various maneuvers. One M.I.T. student tried this with computer aid in data reduction, but the resulting resolution of the bat's position was too coarse. Sixteen millimeter motion pictures proved more useful. The directional beaming of the orientation sounds is a major problem in such measurements; signals at unfavorable angles are 20, 30 or more dB below the level straight ahead. Directional emission patterns are strongly frequency dependent. Since signals have gradual onset and decay, precise time reference points are difficult to locate within them. The frequency sweep should be helpful, in theory, but no one has yet used it effectively for such temporal comparisons in multi-channel recording. But all these problems should serve not to discourage, but to challenge us in designing improved experiments.

Phase or time measurements (the two are readily convertible) may well need to be improved radically in order to investigate relevant possibilities concerning precise "memory" or comparison between emitted pulse and returning echoes. Here we need a high level of engineering talent to develop the precision of measurement necessary to analyze what animals do in the course of echolocation behavior.

Transducers need to be more sensitive and smaller in size without sacrifice of signal-to-noise ratio. It would be helpful to have both highly directional and also non-directional microphones and loudspeakers for different experiments. They must be broad band, and as nearly as possible uniform in sensitivity over the frequencies used by the bats under study. If we had as good transducers for the ultrasonic frequency range, in air, as we do for the human audio range, our experiments could be greatly improved.

Radio telemetry is already being used for simple location and tracking of bats over distances of some miles under natural conditions. One always wants more range per gram weight and per day of battery life. Telemetry orientation sounds, if of sufficiently high fidelity, would permit much improved experiments with false echoes. But for this purpose microphones would have to be reduced in size and weight by a very large factor -- perhaps on the order of 100 fold.

Directional patterns of emission of sonar signals are urgently needed. I suspect the higher frequencies in the orientation sounds of bats of the family Vespertilionidae are concentrated into roughly as narrow an angular beam as the CW portion of the Rhinolophus described by Moehres and his colleagues. In addition the lower frequencies are more broadly distributed. This frequency dependent directional pattern may be significant to the bat, as for instance for obtaining directional information. But this whole topic needs much more thorough study. Likewise these directional patterns of auditory sensitivity would be helpful in evaluating the several ideas discussed at this symposium.

In brief I feel we need better and more intensive investigations before we can hope to understand animal sonar systems adequately. But as far as I can judge we have been more or less on the right track (or tracks).

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DISCUSSION

par

J. C. LEVY

Point A.

Je n'ai jamais dit que l'animal réagissait seulement à une configuration connue, j'ai dit simplement qu'il essayait de reconnaître une configuration familière. Dans le cas contraire, la réaction de l'animal peut être la crainte ou la curiosité.

Points B et C.

J'aurais dû préciser encore deux réactions autres que l'attaque ou la fuite.

Hésitation ou protection par immobilité.

Point D.

Observation valable, mais même si la supposition de l'évaluation de la distance par mesure de l'intervalle, émission-écho, n'a pas une portée absolument générale, elle reste valable comme exemple.

Peut-être ai-je cédé à l'anthropomorphisme contre lequel je voulais précisément mettre en garde mes lecteurs.

Point E.

Le paragraphe incriminé se rapporte au paragraphe précédent qui donnait comme exemple, le cas d'un obstacle à éviter. Le paragraphe parlant du Dauphin mentionnait bien : "dans ce cas".

Il y a là un simple défaut d'attention du commentateur.

Point F.

Ce paragraphe est peut-être "spéculatif" mais je n'ai jamais prétendu qu'il s'agisse d'une thèse.

Notamment, je n'ai jamais dit qu'on mesurait la vitesse d'une locomotive par l'effet Doppler de son sifflet, il ne s'agit que d'une impression subjective, purement qualitative.

Point G.

Peut-être certaines expériences infirment-elles mon affirmation, mais cette dernière, si elle n'est pas universelle, a sûrement une portée très générale.

Je note enfin l'absence totale de commentaires sur l'essentiel de ma conférence portant sur le projet d'expérimentation.

DISCUSSION

by

J. W. R. GRIFFITHS

As an engineer contributing to this discussion it seems to me that I should concentrate my remarks on the experiments suggested by the author rather than plunge into the turbid waters of animal psychology, the subject of the first part of the paper. However, I hope I might be permitted one observation. As far as I understand it, the author is making a case that quantitative reasoning is absent in nature and that an animal proceeds on the basis of the recognition of forms. This conclusion is illustrated by a number of examples in which no conscious computing takes place but I cannot believe that this excludes any form of computing. If this were so, the number of stored pictures which the animal was required to recognize would be extremely large to get any sort of accuracy, and it seems much more reasonable to suggest a quantitative reasoning even if it is, through habit, carried out unconsciously.

In the second part of his paper the author states two points of superiority of animal sonar systems.

- (1) Capability of synthesizing a large number of signals in order to manoeuvre among obstacles

- (2) Capability of detecting an object even though the signal may be intensely jammed by the environment.

Man-made systems can synthesize a large number of signals and the present tendency in design is towards such systems. However it is not merely the generation of such signals which is important but the ability to utilise the intrinsic information. What is the most startling thing about the animal's sonar system is the ability to resolve targets placed closely together (Ref. 1) in spite of the relative small receiving aperture when measured in terms of the wavelength used. Accuracy of location can be predicted from small apertures by presently known theory if the signal/noise ratio is good, but resolution i.e., the distinguishing of objects placed relatively closely together, is quite another matter.

It would seem that the first experiment suggested by the author is a very vital one and I am surprised that it has not already been carried out. The work described by Kellogg (Ref.2) in his book 'Porpoises and Sonar' got very close to this and perhaps by now he should be able to give us some further information of experiments of this kind. The second experiment proposed will determine the accuracy in range but not the resolution since the objects have a wide angular spacing. I feel that the experiment should if possible be modified to produce the angular and range resolution by the use of several similar targets only one of which provides the right type of stimulus. Kellogg in fact does state in his book that the porpoises were much poorer at locating fish thrown in the pool when he had in the pool his network of vertical poles spaced 8 feet apart.

I feel the experiments endeavouring to fool the animal with

a playback of its own voice are unlikely to succeed. Previous experimental efforts endeavouring to jam the animal's sonar have been unsuccessful, as Levy himself has pointed out, and although there is the difference that the animal will still have some control over the echo e.g. the repetition frequency will be determined by it -it is likely that the character of the signal will be altered in such a way that the animal will ignore it. One only has to look at the complex structure of an echo from an object in both time and space to realise how difficult it would be to reproduce this by a single transducer in the water. However this is no reason for not trying!

When a dolphin is approaching an object it oscillates its head from side to side, presumably in so doing it gains further information from the modulations it imposes on the echo. I would be interested to hear of any experiments to determine how important this mechanism is.

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DISCUSSION

by

D. R. KENSHALO

In discussing Dr. Levy's paper, I have encountered difficulty in translating his concept of how stimulus-response relationships are mediated by the central nervous system into terms which I understand. I have the general impression, however, that his concepts are far more mechanistic than my own. Furthermore, his concepts do not seem to permit the degree of plasticity in behavior for which they must account. For those reasons, I shall confine my comments to the experiments which he proposes.

One of the most difficult tasks that I face is to design experiments which meet two criteria. The first is that I have a reasonable chance of retaining control of the experiment for, as any comparative psychologist can testify, when one works with subhuman species, it often appears that the animal tries everything it can to defeat the purpose of the experiment and the experimenter. When this happens it can only mean that the behavior of the animal is not under sufficient control of the experimenter to permit the measurements which are desired. The second main criterion which I strive to achieve is that the results will be clear-cut and capable of reasonable interpretation.

Dr. Levy has outlined his approach as one in which the animal is asked about its powers of acoustic discrimination. The first two experiments are designed to test the acoustic depth (distance) perception of the dolphin. The third experiment proposes a test of the hypothesis that the dolphin uses the Doppler effect, as does man-made sonar, to estimate the speed of closing or opening with the target. A fourth experiment may be described as one concerned with jamming. The information which these experiments are designed to yield would provide a considerable advance in our knowledge of the auditory capacities of this marvelous animal. However, I am not as daring as Dr. Levy, for I feel that we should take a few small steps, or make a few preliminary measurements, before we depend so heavily upon the complete cooperation of the animal. Of course, this caution may be attributed to my lack of a close acquaintance with dolphins, as experimental subjects, and my possibly prejudiced attitude against subhuman experimental subjects, in general.

In the two acoustic depth perception experiments, Dr. Levy has suggested that measurements be made of, first, the distance that a target must be in front of a background in order for it to be detected as distinct or separated from the background and, second, how much closer one of two identical targets must be in order for the dolphin to reliably discriminate it as being closer.

In the first experiment, in psychophysical terms, he is asking the size of the Δ_D , where Δ_D is the difference in distance from the animal of the target and the background. In the second experiment he has placed two targets at acute angles to the sagittal axis of the dolphin and asked essentially the same question, for the dolphin to determine which one is nearer. It appears, therefore, that the first experiment is really a special case of the second or vice versa, depending upon one's point of view. Here, I assume that all targets are of the same material. Otherwise, we would have an entirely different problem--that of how a dolphin can detect differences in texture, which, in itself, is an interesting problem.

These two experiments, which appear relatively straight forward, may have some knotty problems which make clear-cut results difficult to obtain, and which may result in only an equivocal interpretation. Consider the possible cues for acoustic depth perception of humans; there are several and the number varies with the type of signal emitted. The simplest sound is a click such as that produced by a condenser discharge into an electronic amplifier and transducer system. Several auditory depth perception cues which may be used by human observers and which may be used by dolphins with this type of signal are: (a) the time interval between the emission and its echo [in water this will vary with, among other things, changes in depth, temperature, and salinity], (b) the relative loudness of

the echo to the emission [attenuation of the sound due to transmission through a medium; the inverse square law applies here], and (c) changes in the pitch of the echo from that of the emission [high frequency components will be attenuated more as transmission plus echo distance increases]. It is relatively easy to investigate the role of each of these when the subject is docile and completely cooperative but the problem is considerably complicated by the free movement of the animal. Sound localization (direction) cues for humans depend upon differences in phase, loudness, and/or temporal onset of stimulation which reach the two ears. It is apparent that the experimenter must have almost absolute control over the animal's movements during tests of depth perception so that localization cues do not confound the results.

The question always arises as to which of the possible cues the animal uses in performing its discrimination task. The simplest of the cues which may be used for depth perception appears to be the time interval between sound emission and the echo return. This provides a starting point in order to obtain measurements of the dolphin's ability to discriminate depth.

In this context the first two experiments proposed by Dr. Levy may be asking how good is the dolphin's memory for temporal events rather than his temporal discriminatory capability, per se. If one tests the

dolphin's ability to discriminate the distance between the target and the background as a function of its distance from the background, holding the acoustic angle of the target constant, I would expect the resulting function would resemble the standard Weber-Fechener function of $\frac{\Delta D}{D} = K$ or to conform to the Stevens Power Law. I do not wish to become embroiled in this controversy at the moment.

In Dr. Levy's second experiment it may be a more difficult discrimination for the dolphin to estimate the distance of first one target, then the other, and finally to choose the closer of the two. I would expect that the function representing $\frac{\Delta D}{D} = K$ would be about the same as that obtained from the first experiment but perhaps show greater variability. I am not at all prepared to insist that the results of the second type of depth measurement will be more variable than that of the first, for the increased temporal lobe development of the dolphin suggests that the animal may be well prepared to handle discriminations of this degree of difficulty.

Dr. Levy has suggested an experiment to determine if dolphins use the Doppler effect to any extent in order to detect relative movement of a target, then suggests that it hardly seems probable. I am prone to agree with him. Since little is known about the ability of the dolphin to discriminate frequency differences,

it is not possible to determine whether the frequency shift due to the Doppler effect is within their capability or not. From the standpoint of a comparative sensory psychologist, it would be of considerable interest to know what acoustic discriminative capacities are enhanced by the unusually well developed temporal lobes of the dolphin brain. Preliminary measurements of the frequency discrimination capabilities of the dolphin, obtained by psychophysical methods, would answer the question of the extent to which the Doppler effect might be a useful datum in dolphin echo location and, in addition, would provide badly needed data about the basic acoustic discriminative capacities of the animal.

The fourth type of experiment suggested by Dr. Levy is one in which the dolphin is induced to accept false echoes and then to modify them until it will no longer accept them. Neither Kellogg (3) nor Griffin and Grinnell (1) have succeeded in their attempts to jam the sonar of dolphins and bats, respectively, with playback of recordings of the sounds which the animals make. Only qualified success has been obtained with white noise applied to bats (2). The question is "Why?" Drawing upon my own experience, when I hear a taped playback of my voice, I am always struck by the difference in its timbre as compared to when I listen to myself as I speak. Audiologists tell us that this difference is due to having or not having bone and tissue conduction from the vocal

cords to the ear. This suggests that the dolphin or bat would not recognize his own voice when played back to him. Furthermore, the artificial signals, voice and echo, occur at random with respect to any vocalization emitted at the moment, whereas echoes from a real target appear to be time locked to the emitted sound. We all agree that the hearing mechanism of the dolphin and bat appears to be superior in many respects to that of humans, yet the human capacity for discrimination of complex sounds is such that one can pick out and follow the score of the first violin playing with a symphony orchestra. It seems to me that any electronic tampering with echoes would require a system of extremely high fidelity in frequency ranges where it is particularly difficult to build good high fidelity broad band receivers and emitters.

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DISCUSSION

by

J. A. LEONARD

Dr. Levy has already dealt with a number of the points raised by the pre-circulated contributions of Griffin, Kenshalo, and myself. To the extent that our three comments showed a remarkable agreement and in view of the excellent manner in which this has been put by Griffin, I think it is unnecessary to re-state the detailed case once more. I would therefore like to take this opportunity to discuss some more general points arising in the context of this session.

It is a truism to say that the collaboration among disciplines is essential and that any progress along these lines is to be encouraged. I myself have frequently benefited from close contact with other disciplines of which only one example is the collaboration between Professor Kay and myself referred to elsewhere in these proceedings. But there are a number of preconditions for such collaboration to be effective. One is that there must be a degree of mutual respect. In practice this means that if I wish to work together with a physicist in order to solve a given problem I must either be prepared to accept his word for statements which come within his sphere of competence, or else I must get down and become familiar with the latest state of the art in that particular area. Conversely, I would expect the physicist to adopt the same attitude.

Now it is perhaps easier for those of us in the biological sciences to take this step than it is for some in the natural sciences. There may be two reasons for this. One is that the public in general, and many natural scientists as well, still find it hard to accept that it is at least possible in principle to apply the same sort of strategy towards tackling problems on the behavioural level as it is towards the material they are more familiar with. And while nobody would surely pretend that our methods of enquiry are perfect, there is by now quite a sizeable body of recorded knowledge about various areas of human and animal behaviour. What is more, there is a good bit of recorded knowledge about the difficulties encountered in trying to arrive at answers which have some basis of fact as distinct from opinion.

But that is not the only difficulty. For even when the natural scientist or mathematician does enter the field on the sort of basis I have suggested he is, more often than not, rightly disturbed by the enormous variability encountered in our data. Variability to an engineer for instance may mean something like a 1 % or 5 % tolerance in specifying the dimensions of a component. Variability to a biologist may imply a range of readings from near zero to three times the value of an average. Hence of course, the unfortunate need to apply cumbersome statistics to our data. Hence the look of disbelief when a physicist examines our kind of data and tries to comprehend the audacity with which we make statements based on averages calculated from widely dispersed data. There are many cases where people coming to our kind of work with a non-biological background have withdrawn because of the apparent meaninglessness of our data, or else where they have sought to distill the experimental situation to such a point that variability became manageable within their conceptual system but destroyed the essential nature of the problem.

Yet there is a distinct challenge here for those coming with a more exact background to build models of behaviour in which variability is made the cornerstone of the system rather than the dust which has to be brushed off. Up to now we have considered this variability as a nuisance and thought of it either as resulting essentially from random perturbation of the system, or else as resulting from the inadequacy of our methodology - an inadequacy which could in principle be reduced if only we could exert better control. Yet variability within and between subjects appears to be so much an essential feature of all biological systems that one feels 'intuitively' the need for some genius who can break through conventional modes of thought and allow us to make use of variability rather than attempt to fight it.

To turn to a more specific point concerning comparative studies. There seem to me two possibly important differences in comparing for instance the echolocation abilities of bats and men. In the first place blind people rarely if ever use their system for pursuit in the same sense that bats do - though I must report that our young subjects at Worcester did sometimes use the ultrasonic device to assist collisions

rather than to avoid them. But in general hearing is used as a clear-path finding system, a straight line indicator or as a sensor for landmarks.

In the second place, I have the impression that the people working with bats regard laboratory performance as indicating minimum levels of performance while the people working with humans have the opposite attitude. If I have been able to follow the arguments correctly bats are on the whole expected to be rather more efficient in the natural situation than in the laboratory, while humans are hardly ever expected to do as well in real life as in the laboratory echolocation studies. Thus as long as one is primarily considering normative kind of studies, i.e. those in which one seeks to find out what the organism can do here and now, it may be as well to keep these difference in mind. This does not mean that humans for instance could not be brought to higher levels of real life efficiency with more training.

Reverting, however, once more to the session on Sonar in the Blind and combining it with our present topic, I would like to end by expressing the hope that there will be more people like Colin Cherry and Donald Mackay who have come over from the more exact sciences to contribute to biology - just as one would want to see more of the people working with animal echolocation joining the field of human echolocation studies. Here at least we can offer one likely advantage: it is surely easier to observe a blind person by walking behind him in his natural environment than it is to fly behind a bat or swim after a dolphin.

DISCUSSION

par

J. C. LEVY

Dans le cadre de mon préambule déjà très long, je me suis seulement attaché à souligner le caractère "subjectif" de la perception chez l'animal. Je ne pouvais pas donner d'explications complètes. Je ne comprends alors pas très bien pourquoi M. Leonard me reproche, non pas d'avoir omis certaines précisions, mais d'avoir affirmé le contraire, et me prête des idées qui ne sont pas les miennes.

Je vais donc préciser les points suivants:

1° Il ne s'agit que de généralités étayées sur quelques faits psychologiques d'observation courante, et non pas "d'assertions" gratuites.

2° La discrimination entre "digital" et analogique est moins simple pour les systèmes biologiques que pour les calculateurs électroniques. Dans le cas du comportement de l'animal, il s'agit sans aucun doute d'opérations analogiques. Je n'ai jamais dit le contraire.

3° Je sais parfaitement que les opérations des systèmes biologiques se situent à plusieurs niveaux, stratégiques et tactiques; j'ai moi-même publié des articles sur cette question.

C'est cette division du travail, existant par ailleurs dans les calculateurs électroniques, qui permet de réduire le nombre de configurations à mettre en mémoire. Par exemple les mouvements de l'animal sont commandés par les circuits nerveux spécialisés, qui sont les mêmes, qu'il s'agisse de fuite ou d'attaque, il n'a jamais été question d'un circuit unique spécial pour chaque éventualité, ce qui entraînerait évidemment un nombre prohibitif de configurations à retenir.

Enfin chaque configuration partielle ne sera jamais reconnue qu'approximativement, ce qui limite encore la capacité de mémoire exigée.

4° J'ai voulu montrer sur un exemple qui est celui de l'extrapolation du mouvement, la différence de principe entre le fonctionnement du calculateur électronique et celui des systèmes biologiques. Je sais parfaitement que les systèmes biologiques effectuent un contrôle permanent et retouchent leurs données d'après de nouvelles observations, si je n'en n'ai pas parlé c'est simplement parce que j'avais estimé que cela n'ajoutait rien à la valeur de l'exemple que j'avais choisi.

5° J'ai dit en décrivant une méthode expérimentale "l'animal est lâché en A", je n'ai jamais supposé que l'on ait à le persuader à demeurer dans une position "statique". Le point A représente par exemple la porte d'entrée d'un bassin s'il s'agit de dauphins, ou une portière que l'animal est dressé à franchir, ce qui est d'une pratique courante au moins pour les dauphins.

6° Malgré cela, je trouve très intéressante l'idée de M. Leonard, d'appliquer mes méthodes au guidage acoustique des aveugles.

EXPERIMENTS TO CONDUCT IN ORDER TO OBTAIN COMPARATIVE RESULTS

by
R. STUART MACKAY

There are a number of experiments which are obviously needed, and some of which undoubtedly are being carried on by workers in various parts of the world. I shall mention a few concepts and experiments which I feel would be helpful and perhaps stimulating to contemplate, but which are certainly not a complete list nor necessarily the most crucial. Several of the following concepts do not necessarily require new experiments, but rather recommend alternative ways of regarding the data from existing experiments.

I. Use of Phase Information

It has become common to display the properties of sound signals by a frequency-amplitude display (sonogram). Furthermore, it is generally assumed that the ear is a frequency analyzing device. For these reasons it is often, perhaps unconsciously, assumed that a frequency-versus-amplitude spectrum, perhaps as a function of time, is a complete or adequate description of a sound signal in all cases. Unfortunately, such a description leaves out kinds of information potentially useful to certain animals.

The frequency and amplitude of a returning echo undoubtedly contain information about the internal and surface structure of a reflecting object, as well as its shape. Frequency analyses are done not only because they contain potentially useful information, but possibly because equipment for performing such analyses is readily available. It should be noted that there is one other parameter which can carry useful information (1,2), and that is the relative phases of the various frequency components in the reflected signal as compared with the emitted signal. These phase changes manifest themselves as a change in waveform without a change in frequency content, and are essentially independent of range.

The phases with which a group of sinusoidal components are combined affect the overall shape of a signal. Thus, for example, if a sinusoidal signal is combined with another sine wave of three times the basic frequency, then either of two major possibilities can result. In one case, the higher frequency will

tend to flatten the peaks of the basic frequency to something which approximates a square wave, and the other phase relationship emphasizes the peaks until the combination has a rather triangular appearance. Though they contain the same frequency components, these two combined signals reach quite different peak amplitudes, and differently affect any nonlinear detector; the triangular wave form, for example, would cause an electric lamp to illuminate considerably more brightly. Apparently these two possibilities can be distinguished by the human ear, at least when the intensity is reasonably high. To some animals, phase information might be sufficiently valuable so that they would have a special adaptation for sensing phase, rather than the phase information being detected incidental to mildly nonlinear functioning in the hearing mechanism.

It is perhaps true that aquatic animals would find phase information more often valuable than terrestrial animals. Sound signals are reflected at any interface where there is a change in acoustic impedance (acoustic impedance being the product of density and the velocity of sound in the medium in question). In air, most objects to be scrutinized by an animal are "hard" with respect to the surrounding air. But in water, one has materials present which are either "softer" or "harder" than the surrounding medium. The strength of a signal reflected from an interface is proportional to the difference in acoustic impedances divided by their sum. Thus two objects in water could give a reflected echo which was equally strong, and contain the same frequency structure, but yet the two objects be quite different. The difference in the two reflections would be that there is a change of phase of 180° in one of the cases.

A very hard object and a very soft object could both be equally good reflectors. But it would be advantageous to a dolphin to be able to distinguish a smooth rock sitting on the bottom of the ocean from the swim bladder in a fish near the bottom of the ocean. Another circumstance where distinction between the reflections

Unfish or Antifish

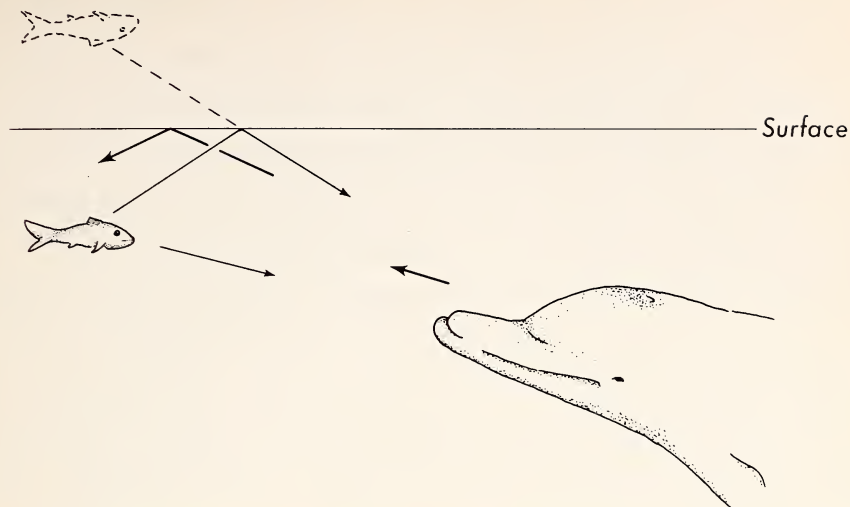
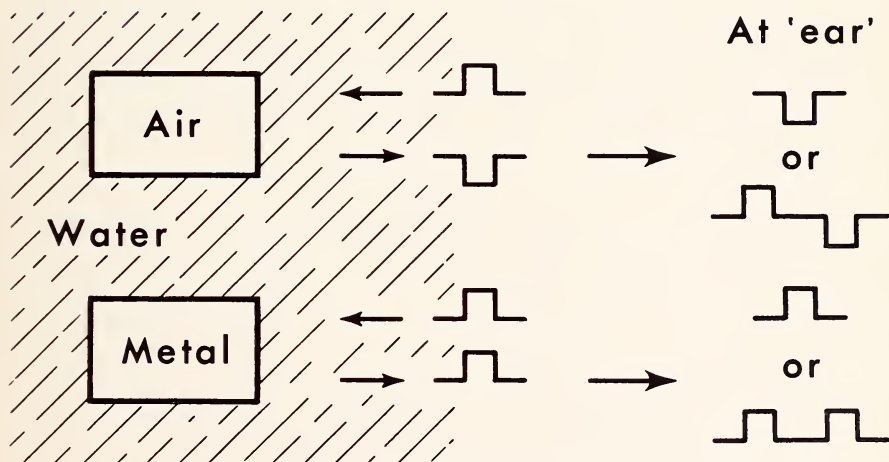


Fig. 1 The reflected image of a fish differs from the direct view by the phase reversal of the frequency components, if the sonic illumination is mostly over the direct path.



Compression pulse emitted, pressure upward

Fig. 2 A pressure impulse is reflected with a 180° phase change at a more-to-less dense interface, and without phase change at a less-to-more dense interface. The hearing mechanism may sense either the reflected pulse alone, or else the emitted pulse followed by the reflected pulse after an appropriate interval.

from a hard and soft object could have survival value is depicted in Fig. 1. Here a dolphin is seen scrutinizing a potential meal ultrasonically. The dolphin will not only perceive the fish, but also its reflection in the surface of the water. If the surface is smooth, the dolphin actually may not be aware of it, because specular effects would carry that echo away from him. Thus in a high speed pursuit situation, it could be of value for a dolphin to have an immediate indication of a fish as distinguished from its reflection or image. Though otherwise similar, the image does differ from the sound signal returning from the fish by the fact that all the frequency components have been inverted at the more-to-less-dense reflection at the surface. Thus this image is somewhat different and might be referred to as an "unfish"; a physicist might prefer to refer to this as an "antifish" because if the fish were combined with the image, they would annihilate each other. In the image, for example, the swim bladder would appear "bright" but "hard". Some ocean bottoms are also capable of producing reflections of this kind. If the sound pulse reaches the fish over the reflection path, then the overall effect can be cancelled under certain conditions of analysis.

The difference in reflection from a hard and soft object might be described in somewhat more detail. In Fig. 2 the situation is depicted to indicate that there is a difference between the echos reflected from a gas-filled cavity and from a metallic object. At the top is shown a positive pulse (a momentary compression) impinging upon a gas-liquid interface, with the reflected echo consisting of a negative pulse of similar amplitude. The same pulse reflected from a very hard object would be similar in all other respects, but would be returned as a positive pulse. It should be emphasized that a positive pulse and a negative pulse are composed of the same frequency components, but differ only in the relative phases with which these components are combined. Thus a dolphin might distinguish a

suited diver from a metallic model of the same, if he could make use of the phase differences in these two pulses. A significant experiment would be to determine if dolphins and other animals can tell a positive pulse from a negative pulse, i.e., if a dolphin can distinguish a compression from a rarefaction. It appears that human subjects cannot make this distinction, or at least not readily. Though perhaps less directly relevant than behavioral data, neurophysiological (electrode) studies on the echo ranging animals with respect to the effects of phase shifts within pulses could be valuable.

A situation related to the previous, which may be more familiar to some, is the fact that a compression pulse travelling down an open-ended organ pipe (or other restricted region) is reflected as a rarefaction, while it is rather perfectly reflected as a compression from the end of a closed organ pipe. Thus it is possible that bats could sense certain openings or orifices by the use of phase information.

In Fig. 2, a simple single pulse is considered for the sake of clarity of explanation. This consideration can be directly applicable to dolphin echo ranging sounds (as opposed to their "conversational" interchanges), since these

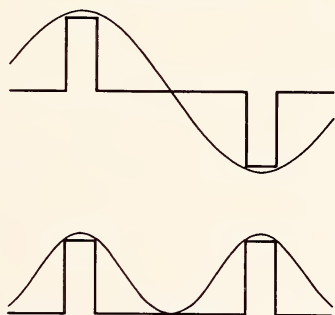


Fig. 3 The fundamental frequency of a positive pulse followed by a negative pulse is half that of a positive pulse followed by a positive pulse. Harmonics form this basic frequency component into the pulse pair. Similar comments apply if one is considering a single isolated pulse pair or if this pair is one of a series of repetitions, though many details are different in the two cases.

generally consist of a few irregular cycles having some net or resultant unidirectional effect from each impulse. Certainly a sound impulse generated by a dolphin would start out with some net d.c. component, since the impulse is generated as a result of energy stored in the form of compressed air being released somewhere. (However, the fact that a liquid cannot sustain a series of unidirectional pulses, since the pressure must average out to the ambient, implies that there will always be some compensating undershoot following each pulse in any actual situation; the undershoot can be relatively long and shallow.) In the case of the regular oscillations found in the impulses of bats, any such consideration as this would still apply to inversion of the various Fourier components that comprise the overall wave train. Also in Fig. 2, there is no indication included of the effect of possible oscillations induced in the structure under study; in some cases these could provide further clues for the animal.

The way in which an animal might use phase information is not essential for this discussion, though a few comments are warranted. In a nonlinear detector (the hearing mechanism of any animal is undoubtedly somewhat nonlinear), one obtains different amplitudes of generated frequencies with alteration of phase or of amplitude of the incoming signal. Thus a frequency-analyzing ear might be sufficient to interpret the phase information in a returning echo, especially if the outgoing signal could be carefully controlled or else monitored. It is obviously possible for any system to tell a positive pulse from a negative pulse by nonlinear action which is rectifier-like if the effect of ringing is removed through combination of the direct and a delayed pulse.

However, another interesting aspect should be mentioned. The animal's sound generating mechanism is undoubtedly not perfectly isolated from his hearing mechanism, and perhaps it should not be. Thus, as is seen in the right hand part of Fig. 2, at the ear one might actually have a positive pulse followed by a negative pulse in one case, and a positive pulse followed by a positive pulse in

the other case. The original pulse is assumed attenuated until its amplitude at the "ear" is comparable to the magnitude of returning echos. Such pulse-pair types apparently can be distinguished by human subjects if the two members of the pair are close enough together. From Fig. 3 it can be seen, as is well known, that the basic frequency component of a positive pulse followed by a negative pulse is half that of a positive pulse followed by a positive pulse, and thus to make such a distinction does not require phase information, but can be done from the different frequency components involved. (In this figure, harmonics would square off the basic frequency into pulses, and correct their relative heights if unequal.) It might be expected that a reflection from a soft object would appear twice as far away and similar to the reflection from a hard object, except for the relationships among the higher harmonics which distinguish these two cases. (Certainly a pure sine wave is not suitable for most sonar purposes.) In general, it can be stated that it is theoretically possible for a frequency analyzing ear to distinguish a hard object from a soft object, though phase information can be valuable in a number of cases; phase information is also especially involved in shape discrimination.

It would be interesting to make tests in which various species would be asked to distinguish between two reflectors which give similar echoes as far as their amplitude and frequency structure is concerned, because of having acoustic impedances differing by the same amount from that of water, but in opposite directions.* The corresponding experiment with bats might require recognizing small openings. In combination with observations of ability to distinguish an isolated compression from an isolated rarefaction, this should give information on the degree of use of phase information. Without going into theories of hearing, if phase discrimination

*Note added in proof: William Evans has taken this suggestion from an earlier discussion and performed the experiment on Tursiops truncatus with quite positive results, to be reported elsewhere in this volume.

is something an animal can do, then the usual analysis of frequency and amplitude which we make to describe the performance of an animal is incomplete and perhaps misleading, or at least partially irrelevant.

One other parameter of a sound source is its direction. Wavelengths used by dolphins are small compared with the size of the melon and thus, there can be lens action or imaging (apparently with variable focus in captive Belugas). Either scanning or multiple sensors thus can contribute to shape identification of a target even if the multiple sensors are similar to the mechanical sensors in our skin. Certainly the lateral line organ in fishes might perform some such functions.

In assessing the acoustic performance of an animal, the sound source can carry information in the form of direction, phase, frequency, and amplitude. To repeat, to make an analysis leaving out some of these may lead to results like that of a chemist who would grind up a cat and make an analysis to understand the animal; it may deal with manageable and important concepts but leave out essentials.

II. Choice of Frequency and Storage Time

A comparison should be made in various species to determine the ratio between the wavelengths used in their sonar systems and the size of their normal prey or food. In Fig. 4 a graph of well known information suggests that an interesting region to explore is the range of frequencies for which the wavelength is comparable with the prey size, and that animals would have a certain advantage in using such frequencies. In this sketch, various resonances and related interactions have been left out for simplicity. It is seen that with very low frequencies a very small signal will be returned from an object. This region of small signal return from objects less than a wavelength in size represents the so-called Rayleigh fourth-power scattering law. If frequencies very much higher than those for which a wavelength is comparable with the object size are employed, then there will be excess attenuation of the sound waves by the medium. Thus for reasons of returning

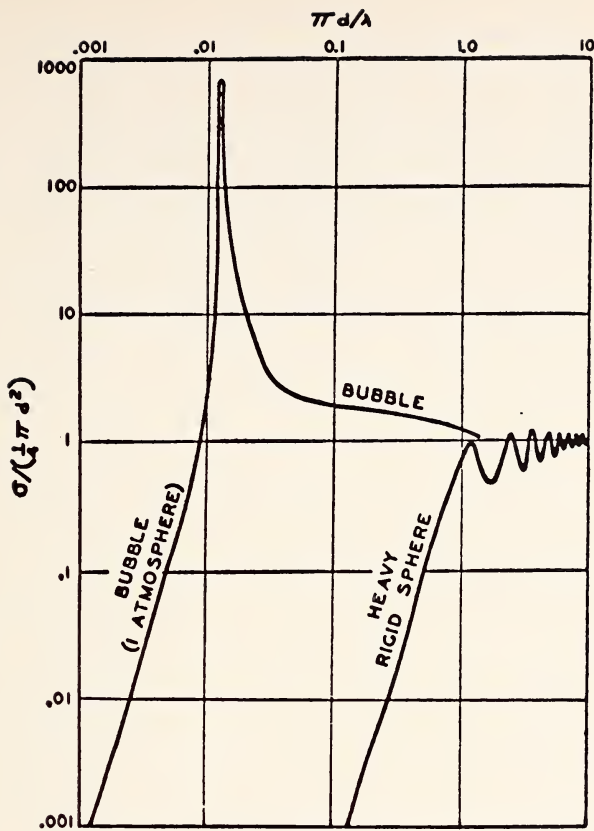


Fig. 4 Well known change in scattered signal from sphere as frequency varies, here shown as apparent target area as a function of circumference measured in wavelengths. The extreme underwater cases are graphed, with a similar situation existing in air. Though this is a simplified hint relative to any biological case, animals employing sonar perhaps should use wavelengths comparable to their prey size to maximize signal, minimize attenuation, and give sensitivity to shape difference upon motion; the various species should thus be considered.

signal strength it might be expected that this intermediate range would be valuable. It is to be seen that in this range of frequencies a small change in size of a spherical object produces a relatively large change in the returned signal. This is a highly simplified case, but it suggests that small changes in orientation of an irregularly shaped subject in this range would produce a large change in signal strength. Thus it would be expected that a bat using such a range of frequencies would have good sensitivity to wing motion of flying prey, and that a signal being returned would have an amplitude modulation envelope strongly dependent on shape if the subject were tumbling. In any actual case, there may be resonances in the object and other effects which will actually lead to much greater intensity fluctuations, but such a simple case does suggest a range of interest.

Some animals could choose to use considerably higher frequencies for which a wavelength would be short compared with the size of the object being explored. This would allow resolution of geometrical detail in the object. Another effect might also be expected, but be somewhat more difficult to explore. It has recently become well known (3) that one can produce a full colored light image of a scene by photographing it in white light and in red light, and then projecting the two images together. In the resulting picture one perceives the various colors, including green, brown, red, etc., all in their correct places. Similarly, the combination of an ultrasonic signal from an animal with the normal ambient noise which covers a wide range of frequencies, might give wide spectrum information about a scene. If the subject animal were projecting a more or less restricted range of frequencies, then an experiment in which most ambient sounds were removed might be seen to degrade performance if such a mechanism were being used. Just as in the optical case, too much white light can spoil the effect, so the fact that loud sounds having a wide frequency range can produce a jamming action does not indicate against such a mechanism.

Especially from the studies by various workers on bats, it appears that animals are able to perceive targets which are, in fact, considerably smaller than one

wavelength across. This means that they must be working with rather weak returning signals. It would be expected that if a very long observation time could be used then a very small object could be sensed. Thus resolving power experiments could be interpreted to give a potentially important parameter of an animal's sonar system. This would be the length of time over which information would have to be collected and stored in order to give the observed performance. It would be interesting to know if a bat integrates and uses information obtained over a full pulse, over a fraction of a pulse, or over several pulses. In the light optical case (4) the degree of discrimination that can be made at low light levels suggests that the effect of quanta impinging upon the human retina is averaged over approximately two-tenths second, and this is often referred to as the integration or storage time of the eye. A similar type of computation could be made for a sonar system of an animal, though the existing experiments might be modified to use targets of differing contrasts (in this case, relative acoustic impedance with respect to the surroundings).

A long storage time does imply a slower information rate to the animal, so it would not be surprising to find pulses acting separately, with an individual duration related to prey size, and perhaps ambient noise.

III. Prey Properties

The possibility that echo ranging animals recognize their prey by inducing characteristic "ringing" in the body of these animals would be most likely if biological tissue showed a high mechanical Q . Then resonances would be sharp and induced oscillations would persist for many cycles. We have made measurements of oscillations in eyeballs and observed Q s of about 4. This is rather low but does give resonant effects. Presumably a worm would be similar, and fish less (except perhaps for a swim bladder). Oscillations induced in prey animals could be studied to clarify possible hunting mechanisms; low Q objects can be recognized as such and scrutinized by animal sonars, but they are not characterized by strong resonant reradiation of certain frequencies.

IV. Possible Single Transducer Systems

One should make accurate observations in various animals of pulse repetition rate as a function of range to target. These might be considered as adjusted to arrange the overall content of Fourier components into an especially noticeable combination, rather than, for example, adjusting the information rate as needed.

But perhaps some animals use another form of sonar that one could conceive, and which would require adjustment of repetition rate. Suppose a compression pulse is arriving back just as the next compression pulse is being generated. At this rate (which indicates range), the generation process undoubtedly feels different to the animal because the noise maker must push harder, i.e., it seems to be working into a higher impedance medium. And the magnitude of the change felt at this particular rate sets in, is a measure of the hardness of the reflector; this constitutes a remote feeling process almost as if a hand were reached out and something touched with a finger. Similarly, in blowing a trumpet, the process feels different if length is appropriate to the tone being blown, which tends to make one blow at that rate. Just as in distinguishing a shorted or an open-ended electrical transmission line, one could not tell a hard object from a very soft one at a different range if only a sine wave were used in testing. In methods considered here, a separate transmitter and receiver are not needed; probably a human hand moved in a jerky fashion in a swimming pool could sense the range and hardness of a distant object. Such a mechanism could be used by animals, and it should be watched for in otherwise puzzling cases. Perhaps certain short range discriminations or schooling in fish relate to this.

V. Observations on Living Tissues

Techniques are now available for exploring various body structures using pulsed ultrasonic energy. The techniques can build up images that are superior to X-ray images when soft tissue structures are involved. The resolution of detail can be quite excellent and, in human subjects, structures such as the vocal cords can be observed under circumstances where they would be totally invisible in a radiograph. (Examples

will be shown.) If one is interested in the sound producing structures in other animals, then it would seem appropriate to observe them using sound, rather than electromagnetic energy.

In this connection, it should be mentioned that in our studies we find that there are extremely rapid postmortem changes. These can take place in a fraction of an hour, and may be due to the generation of minute gas bubbles. In any case, this suggests that one not try to study sound producing or analyzing structures only in preserved animals.

One type of observation that is appropriate is to measure the velocity of sound in various living tissues, such as the melon of a dolphin, and also the acoustic impedance. The former has been done in some other animal tissue by transit time measurements, and the latter can be done by measuring the magnitude of reflected sound energy when passing from a material of known acoustic impedance such as water into the tissue of the animal. Tissue attenuation is also important since acoustic lenses, unlike most light lenses, also modify their output intensity distribution through variable absorption.

Another type of observation might be to find the site of certain biological sound sources, this being a special problem in some of the aquatic animals. A number of sound detectors affixed to the head of the living animal might indicate the location of a sound source by the difference in arrival time of each impulse at these several sites. This might be considered as analogous to the localization of an earthquake by the difference in arrival time at three stations, or the localization of a moving aquatic sound source by noting the arrival time differences of random pulses at four locations. (The position of flying animals might similarly be recorded for observations in the previous section.) Methods which might be invoked in making sound production observations will be mentioned in the next section. Sonic mechanisms may be quite different in different animals, even if one restricts attention to the whales.

VI. Telemetric Observations on Unrestrained Animals

Small radio transmitters which can telemeter signals from untethered animals

in air or in water have become perfected in recent years and gone into routine use (1,2,5,6). For aquatic animals, a sound transmitter can either transmit a signal directly at the original frequency or else as a modulation on a somewhat higher frequency. The original signal can instead be rectified, to determine its time of arrival, without the necessity for complex wideband circuitry. When affixed to the head of an animal, such a transmitter could indicate more exactly the sounds that the animal generates, and what it hears from returning echoes and reverberation.

SONIC TRANSMITTER

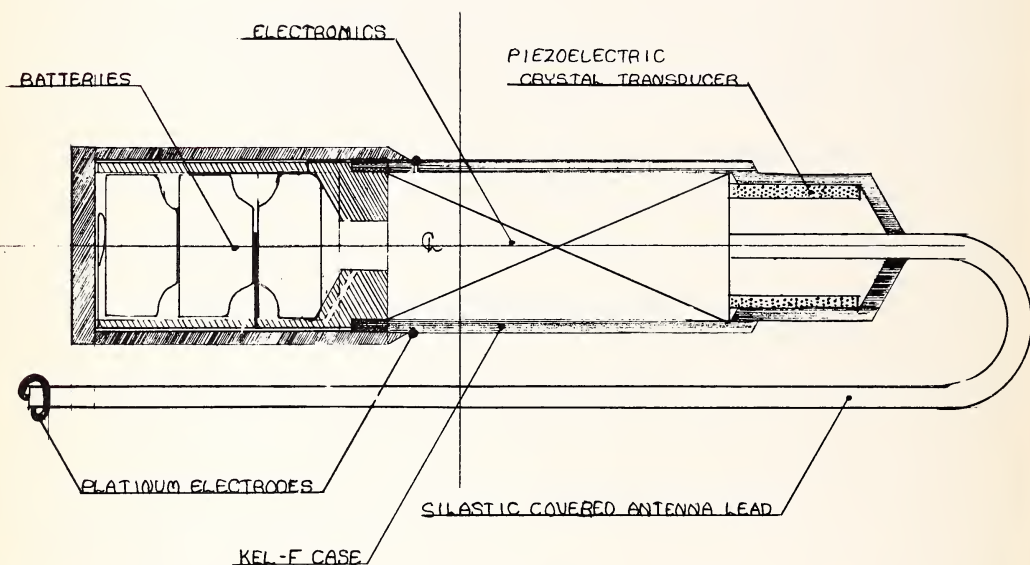


Fig. 5 Sound sensing transmitter that has been built for ingestion by dolphins; the diameter is approximately 1 centimeter. Operation has been satisfactory, though in this particular design forces applied to the antenna wire sometimes introduce forces into the sound transducer, with accompanying transmission of noise.

In acoustic discrimination tests, it is possible thus to monitor the absolute intensity of a generated signal being presented to the animal, in spite of variations over the tank. For sonar performance tests, such methods make possible absolute source strength measurements of impulses from the animal. Representative arrangements are shown in Figs. 5 and 6, where there is depicted a transmitter type which has been fed to Tursiops truncatus to determine internally generated sounds.

A transmitter of the type shown in Fig. 6 can be placed near the head of an animal to indicate the pattern of returning echoes. There is no guarantee, however, that signals will be concentrated upon the transducer in exactly the same way as they are directionally perceived by the hearing mechanism of the animal. This circuit (related to Fig. 14 of Ref. 1) filled a 50 foot tank of ocean water from all positions, with a battery life of about one day. The very small size of the transmitter was dictated by the fact that a dolphin gastrointestinal tract is in places smaller than that of a human, and the unit was ingested. Increase in transmitter size with external placement improves all aspects of performance. For applications where a higher range of frequencies is to be transmitted, there are three choices. One can use the same arrangement with a carrier frequency of about a megacycle, but electrical "skin depth" considerations then limit the transmission range to a value that requires careful arrangement of the receiving electrodes in the tank. One can instead dispense with the carrier frequency and transmit the acoustic frequencies directly after conversion to an electrical signal; troublesome interference can be eliminated with a high pass filter at the receiver input. The third alternative is to use the same circuit for acoustic transmission in the megacycle range. If the output electrodes are attached to a titanate cylinder similar to the input unit, satisfactory transmission is achieved. With reasonable care, because of the frequency difference of input and output, feedback will not cause self-oscillation.

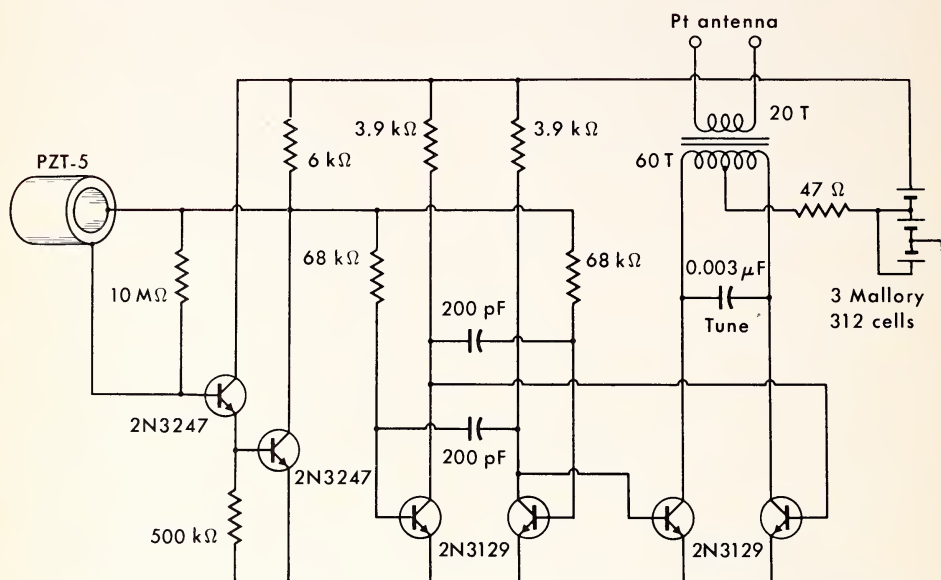


Fig. 6 Circuit of transmitter in which relatively low frequency sound signals frequency modulate an oscillator whose output stage drives a pair of electrodes. The same circuit type can work in other sound frequency ranges, and for the transmission of electrical and other signal types under water. Similar circuits with a higher radio frequency can also be used in air.

Similar circuits can be used to transmit such parameters as electromyographic potentials generated during vocalization, or cochlear microphonics indicating what the subject actually "hears". In such cases, the electrodes feed their signal to the input circuit rather than monitoring the voltages from the sound transducer. Thus one might use such arrangements to monitor the cochlear microphonics from a seal both in and out of the water, and during rapid changes in pressure. The best way to determine which structures are active during sound generation may be the use of fairly deep electrodes which can now be placed in dolphins under anesthetic.

In general the circuits for studying animals in air are simpler. Using batteries such as the Mallory 212, transmission of physiological information within the laboratory can be achieved with transmitters weighing under a gram and occupying a volume less than one cubic centimeter. Thus the ear motion of a horseshoe bat might best be followed with radio telemetry. However, due to the very small size of many of the animals of interest, passive methods in which no source of power is carried by the animal are of special interest.

The signal from a radar set is strongly returned from a piece of wire a half-wavelength long, and circular polarization minimizes the effect of orientation changes. The signal can be obscured by the usual reflections from nearby large objects. Cyclic detuning by a periodic physiological variable leads to a twinkling at the receiver which helps identify the signal of interest. We are working on experiments to determine if this is a useful way for tracking an animal, with limited facility for following the frequency of some variable of interest.

We are also testing several promising systems which are intended to return a radar signal at a slightly offset frequency so that the receiver can be detuned and reject the clutter of background reflections. One compact unit under test uses a resonant loop across which is connected a tunnel diode in series with a condenser. Power at the transmitter frequency induces a voltage into the loop to charge the condenser through the diode. Following this, the condenser serves as a power source to produce extended oscillations in the loop via the negative resistance

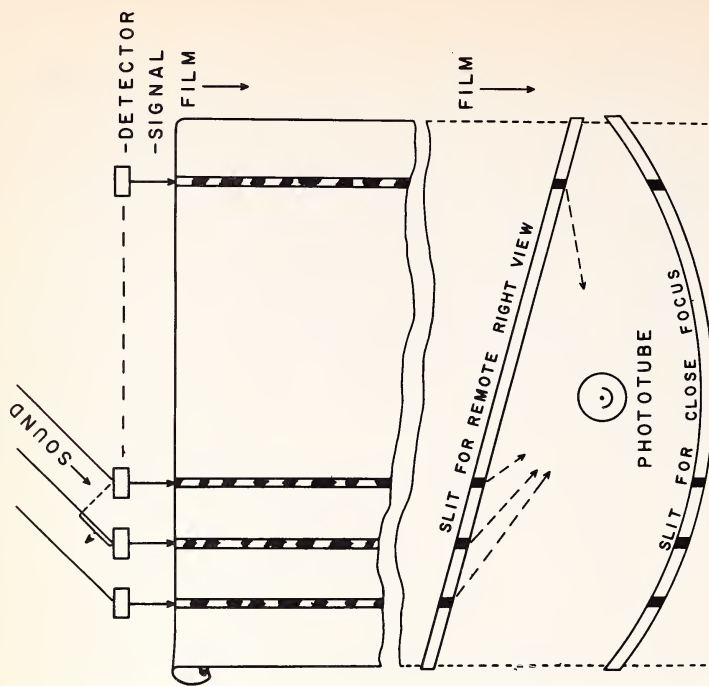


Fig. 8

Arrangement of a theoretical experiment which suggests that a single click can define the structure of the whole field if the time course of echoes at several locations is known. This suggests that it may not be unrealistic to assume that extremely high performances are theoretically possible, though the above neglects all noise.

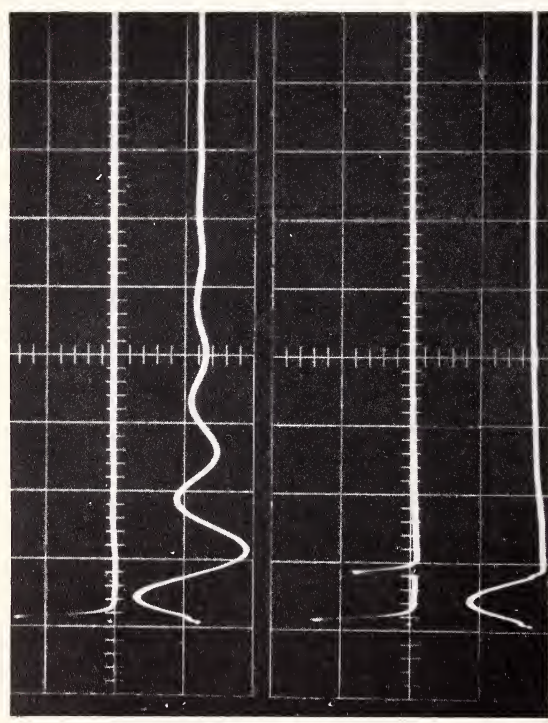


Fig. 7

Top: Oscillogram of ringing of resonant system in response to an applied impulse shown on first line.
Bottom: A suitably spaced and energized pair of pulses results in a sharp response of this system, which is suitable for timing purposes. The Q of this system was relatively low, as can be seen by the few cycles of oscillation before cessation.

action of the diode. The returned pulse is delayed, a prompt shifted return requiring the radar signal to activate a local oscillator on the animal. Ranges are presently uncertain, but in all cases transducers can cause frequency modulation for telemetry in addition to tracking.

Continuous versions of these intermittent transmitters can be visualized for use with sound signals. However, passive transmission may not prove appropriate with certain transducers, e.g., there is some indication that a corona discharge might make a very small, though noisy, high frequency microphone. In that case, active transmission in the laboratory presently seems indicated.

VII. Use of Double Pulses by Echo-Ranging Animals

It appears that many animal types generate not periodic pulses, but periodic pairs of pulses. This has been noted in the sounds produced by a number of fish. Norris has commented upon it in Tursiops truncatus, and Poulter has mentioned the occurrence of such sounds in sea lions. From the records published by other workers on various terrestrial animals, it would appear that many species do this. Though in some observations this may be an artifact due to the reception of the direct signal and its reflection over a different path, this may prove to be a very important acoustic mechanism for some animals. Any hearing mechanism must consist of a compliant structure upon which the sound impinges, said structure being loaded by the mass of the adjacent medium. Thus, an impulse will set the entire structure into vibration, which would tend to obscure further information for an appreciable time after each impulse, i.e., during "ringing", returning sounds would be obscured. (The human ear drum is known to vibrate through several cycles following an impulse.)

At the top of Fig. 7 is seen the ringing of a damped resonant system in response to an impulse. Below is seen how two almost identical pulses separated by $1/2$ cycle of the mechanical system can cancel to give sudden silence; other combinations of pairs of similar or dissimilar signals can cancel also, including alternating impulses of unequal amplitude. At least superficially, the dolphin signals seem

the most likely to be of the correct magnitude to employ such a mechanism.

If a variable tension mechanism is present in the hearing receptor (as in the human), then a variable spacing is needed to give a quiet period after each sound burst. This may be a way for an animal to discriminate against the jamming action of signals from other nearby animals, whose impulses would just "ring" into background noise.

Not only could arriving echoes each cause ringing, but the animal's sound source might itself ring. To achieve quiet after his own signal is generated, he might apply four impulses to his sound source, to give out two sharp clicks. These would then assure a sharp signal without ringing for each returning echo, i.e., each echo would be a double pulse giving a single sharp pulse from the ear. As techniques advance, it may be possible to search for neurophysiological evidence of all this, using telemetry.

VIII. Various Theoretical Considerations

In appraising animal performance, various theoretical limitations and possibilities should be considered. Frequency modulation (limited to an octave to avoid harmonics) during a pulse gives an amplitude envelope strongly dependent on target size and shape. FM also gives difference frequencies dependent on target size, and a different tone in the two ears dependent on target bearing; head orientation during pulsing should be studied. Perhaps electrode studies in which different tones were played into the two ears would yield useful information.

Sounds crossing a water-air interface might be mentioned. It is well known that the intensity of a sound wave crossing such an interface is attenuated by a factor of approximately 30 decibels. However, it is also true that pressure, including sound pressure, must be the same on the two sides of the interface. Thus a perfect pressure transducer might be expected to give the same indication after immersion as it did while still in air, when responding to a sound source in the air. There

are actually no perfect (infinitely stiff) pressure transducers, but some animals might develop systems approximating one. In an experiment to test this idea, a sound source was placed outside of an aquarium. A piezoelectric sound transducer gave approximately the same signal whether in or out of the water.

As indicated in Fig. 2, a sound wave and its reflection in air are in phase. Thus the sound pressure transmitted into water could be twice that otherwise existing in the air. By the same argument, the sound pressure communicated from water into air might be expected to be approximately zero. This apparent asymmetry has obvious implications for animal performance. It also explains why so much airborne noise is picked up by hydrophones in dolphin tanks. With regard to suggested animal experiments, these facts suggest measuring the acoustic impedance of the hearing organs (where identifiable) in a number of species to see if any having some need for hearing in and out of the water (the former not requiring maximum sensitivity) have equalized reception by merely developing a stiff sensor.

One might consider how much information about one's surroundings might be obtained from a single click, or conversely, how fast (how many clicks) would be required to explore the full surroundings, neglecting noise. With such an estimate, one might be better able to appraise the performance of an animal without matching an experiment to an impossible result. Leaving out specular effects and the necessity to surround an object in order to catch all echoes and view all subject points from all directions, the following gedanken experiment suggests a limiting performance capability in terms of a system that is perhaps realizable.

Consider a single pulse given out and the complete time course of echoes returning being recorded separately at several positions (Fig. 8). At each "receptor station" sound intensity is recorded as a strip of variable blackening on a film. This film is later replayed back through various masks on to a photo-cell to effectively introduce different time delays between stations. It is seen

Specular Reflections From:

Corneal Front Surface

Corneal Back Surface

Lens Back Surface

Posterior Pole Of Eye

And Orbital Fat



Fig. 9 Photograph and diagram depicting a problem common to all high resolution sonar systems. This is an image of the author's eye using pulsed 15 megacycle ultrasound. With a simple scan the entire structure is not visualized, but only parts perpendicular to the beam.

that the time course of echoes from various directions can be followed, all other signals averaging out as noise, and one can even focus attention on a particular place with a curved mask. It would appear that a single pulse is able to define all boundaries, and one can imagine neurological connections that might produce a similar result in animals with the help of a short-term memory.

In any real case, not all echoes may return to the receiver because of specular effects. Fig. 9 includes a photograph of a biological object scanned by a sonar system; not all parts are visualized unless a more complicated scan pattern is used. Scanning by an animal may not simply be to cover an extended area, but may be to visualize all points of the subject from a variety of directions. The motion of animals should be followed to discover the details of what is being "seen", when they are exploring targets large enough to show such effects.

In explaining the performance of animal sonars, one must assume that all theoretical possibilities are employed to make the signal "sound good" to the animal. In laboratory work, we find that time-gating can discriminate against back-scatter in the medium (in some cases neglecting multiple scattering), and we should assume that an animal is able to ignore certain kinds of information that does not appear interesting. Similarly, phase coherence of an interesting part of a signal between a number of clicks in a train could be used for discrimination in a situation that might appear impossible when analyzed impulse by impulse.

These are not necessarily new thoughts, but as the superficial aspects of performance are stripped away, then more sophistication of analysis must be used in our interpretation of all experiments.

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ABSTRACT

The importance of analyzing phase information in echoes, e.g., for bats to find openings and dolphins to distinguish swim bladders from stones, rather than just scrutinizing frequency and amplitude is emphasized. Experiments to study this are suggested, as well as the choice by the animal of frequency and integration time. Also discussed is the exploration of the acoustic properties of the tissues in both the prey and predator animals. Some methods for making telemetric observations on unrestrained animals, both aquatic and terrestrial, are given. The possible importance of double pulses, scanning pattern, and other basic limitations on sonar systems is presented. Understanding of the way animals deal with these factors in some cases suggests new experiments, and in other cases may require reinterpretation of existing data.

DISCUSSION

par

J. C. LEVY

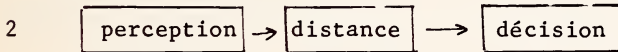
La communication dont il est question a pour but de préconiser quelques expériences relatives au sonar animaux.

Qui dit expériences à faire, dit problèmes non encore résolus. Le préambule ne sert donc qu'à poser le problème et ne doit pas être considéré comme une thèse reposant sur des faits scientifiques rigoureusement établis, mais comme une mise en garde contre des idées trop simplistes et trop "antropomorphiques". L'animal ne travaille certainement pas comme une machine, et son processus mental doit pouvoir être comparé à celui de l'homme, dépourvu de tout esprit scientifique et privé des notions les plus élémentaires de calcul.

Notamment, je pense que l'animal n'est pas capable "d'explicitier" la notion de distance. Autrement dit, quand il s'agit pour lui de prendre une décision liée à une mesure de distance, son processus mental doit pouvoir être représenté par le diagramme suivant:



et non par celui-ci



Cette idée n'est pas une "assertion", elle n'a à ma connaissance encore fait l'objet d'aucune expérimentation précise, et je n'ai fait que l'appuyer sur des faits psychologiques d'observation courante qui à défaut de preuves constituent une bonne présomption, d'une notion que l'expérimentation proposée pourra contribuer à préciser.

La difficulté du problème n'a pas échappé aux lecteurs de mon papier, peut être ne me suis-je pas assez étendu la-dessus.

Faute de données numériques analogues à celles utilisées dans les appareils de fabrication humaine, il y a correspondance purement empirique, d'une configuration spatio-temporelle de signaux d'entrée, avec une configuration spatio-temporelle de réactions motrices.

Si l'on admettait qu'à chaque configuration d'entrée doit correspondre une configuration de sortie, on serait vite conduit à des conclusions absurdes. Le nombre de configurations possibles est en effet incommensurable, aucune mémoire ne pourrait en stocker le nombre nécessaire.

La solution du problème consiste à admettre comme il l'a déjà été proposé par de nombreux auteurs (1, 2, 3) que chaque configuration générale est constituée par un assemblage de configurations "préfabriquées" dont le nombre est accessible à la mémoire. La meilleure image que l'on puisse donner de cette composition est le langage humain, qui avec un nombre de mots et de règles de grammaire accessibles à la mémoire permet d'exprimer un nombre d'idées pratiquement infini.

Il est hautement vraisemblable que chez un animal supérieur tout processus procède du même principe. Seulement l'animal ne disposant pas de langage ne peut pas nous l'expliquer.

L'anatomie et la neurophysiologie montrent que chaque organe est relié à une aire de projection déterminée du système nerveux central. Il est peut être difficile de prouver rigoureusement que chaque per-

ception élémentaire, ou que chaque mouvement élémentaire, correspond à un circuit spécialisé. En effet, il n'est pas possible, de tester simultanément un nombre suffisamment grand de cellules, mais toutes les expériences partielles faites (trop nombreuses pour être citées ici) confirment cette hypothèse.

Selon notre comparaison avec le langage humain, chacun de ces circuits correspondrait à un mot, et toute configuration générale ne consisterait qu'en un assemblage de ces mots, ceci selon des processus en cours d'étude par moi-même.

D'autre part, la comparaison entre le comportement de l'animal et les possibilités d'utiliser un langage nous rapproche de la communication de M. J. Bastian qui est discutée dans une autre séance de ce colloque.

Pour le moment, faute de résultats expérimentaux que nous désirons justement pouvoir préciser, nous en sommes réduits aux conjectures.

Nous n'avons qu'une certitude, mais une certitude négative, l'animal ne connaît pas la métrique et la notion de distance exprimée sous forme de grandeur mesurable lui est totalement étrangère: elle intervient pourtant dans son comportement, mais l'animal peut-il d'une façon ou d'une autre "expliciter" cette notion, c'est-à-dire, par exemple, la communiquer à l'un de ses congénères?

Il y a là encore des sujets d'expériences que je ne saurais imaginer moi-même sans l'aide de spécialistes.

Je vais faire une autre digression à propos d'une réflexion faite dans sa note critique par M. Leonard.

Les circuits nerveux que j'utilise dans le modèle faisant l'objet de mes études, sont des circuits statistiques dont le principe est le même que celui des réseaux aléatoires de Von Neumann (5).

Ces derniers sont constitués d'éléments booléens, c'est-à-dire susceptibles de n'occuper que deux états, excitation ou non excitation. L'état d'un ensemble d'éléments est alors caractérisé par la proportion d'éléments excités. Soit N le nombre d'éléments constitutifs du système et E le nombre d'éléments en état d'excitation. L'état du système est alors caractérisé par une proportion.

$$P = \frac{E}{N}$$

cette proportion peut prendre une suite "discrète" de valeurs

$$\frac{1}{N} - \frac{2}{N} \cdots \frac{E}{N}$$

Mais si N est très grand, l'écart entre deux valeurs consécutives peut être rendu aussi petit qu'on le désire. On peut donc dans le cas des systèmes biologiques composés d'un très grand nombre de cellules, admettre que P varie d'une façon continue, il s'agit alors d'un système analogique.

Il me reste à donner un complément d'explication à la suite d'une remarque faite par M. Leonard. Je n'ai jamais supposé qu'il faille persuader l'animal de demeurer dans une position statique, en fait deux cas sont à distinguer:

- 1/ Dans le cas des mesures ou comparaisons de distances: le dispositif opératoire est statique l'animal est "lâché" en A; A pourra par exemple être la porte d'entrée du bassin, s'il s'agit d'un dauphin,

ce point doit être assez bien défini dans l'espace, mais pour ce qui est de l'époque, l'animal peut franchir la porte, quand bon lui semblera.

- 2/ Dans le cas des mesures de vitesse radiale: l'expérience commence à un instant précis qui est à la disposition de l'opérateur, en attendant l'animal doit être maintenu en place, mais l'endroit où il se trouve n'a pas besoin d'être défini avec la même précision, on peut donc le maintenir dans un enclos, qu'il ne quittera que quand l'expérience commencera, de plus l'opérateur peut choisir le moment favorable pour commencer l'expérience alors que le sujet se présente dans une position adéquate.

De toute façon, les expériences que j'ai préconisée postulent un certain dressage de l'animal, il n'y a aucun doute que ce dressage est praticable avec les dauphins, mais je ne peux pas garantir qu'il le soit avec les chauves-souris.

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XI

Discussion générale

General discussion



SOUND ORIENTATION AS SEEN BY A PSYCHOLOGIST

amuel by
D. R. KENSHALO

For the past five and one-half days we have received a very concentrated exposure to research which has been done on the use of emitted sounds by various species of animals apparently for the purpose of spatial orientation and target location. Before starting a general discussion of the results of this Symposium, it might be helpful to review the highlights of these presentations, organized in a different way, against a background of the previous work on this topic. A number of questions have been raised by the research presented here and some of these will be enumerated. In addition, the contribution of the various disciplines of engineering, physics, biology, and psychology to the problems of sound orientation have been the subject of informal discussion.

BACKGROUND

The use of echolocation by bats to capture insects and avoid obstacles was first suggested by Spallanzani (5) during the latter part of the 18th century. Other suggestions, not involving echolocation, were made by various people as to how bats performed these feats when vision appeared to be precluded by the level of illumination. But it was not until Griffin (1), in the United

States, and Möhres (4), in Germany, began their pioneering studies of bats, which confirmed Spallanzani's suggestion, that a clear picture was obtained of how Myotis l. lucifigus and Rhinolophidae succeeded in accomplishing their feats of obstacle avoidance and insect capture.

Kellogg and Kohler (3), only 14 years ago, were the first to suggest that the bottlenose dolphin, Tursiops truncatus, may use a sonar similar to the echolocation mechanism of bats in order to accomplish the same result. Since then, much of the research effort, using this species, has been directed toward a study of the conditions under which echolocation occurs and to semi-naturalistic observations of their echolocating discriminatory capacities in the capture of food and the avoidance of obstacles.

RESEARCH REPORTED AT THIS CONFERENCE

In order to review the results of investigations which have been reported at this conference in a systematic way, it is convenient to divide them into six main categories. These are: (a) surveys of sounds produced by various species; (b) physical, anatomical and engineering approaches to the mechanisms of sound production and reception by various species; (c) engineering models of sonar systems and their analyses; (d) studies of discrimination capacities; (e) social communication among echolocators; and (f) neurophysiological investigations of processing of auditory signals by the higher nervous centers of echolocators. These are not discrete categories in that

there is a considerable overlap of particular papers among the several categories.

Surveys of Sound Produced by Various Species. Dr. Pye has reported that the ultrasonic pulses produced by over 65 species from 13 major families of Chiroptera have been collected and subjected to spectrographic and oscilloscopic analysis of the frequency and wave form of the sound pulses. There appear to be four basic frequency contours of the sound pulses which can be derived from a single frequency-time pattern by gating it at various sections of the pattern. These four main frequency contours are a frequency sweep (FM) from high to low, a constant frequency, and two combinations of these in which the first is a constant frequency followed by an FM shift to lower frequencies and the second is an FM sweep, from low to high frequencies, followed by a constant frequency. The last type of frequency contour has not been found in any of the species which he investigated.

Dr. Neuweiler reviewed the literature for evidence of echolocation in various terrestrial forms of birds and mammals and his list was extended to include aquatic mammals by myself and further extended by Dr. Webster to include several species of insects.

Physical, Anatomical and Engineering Approaches to Mechanics of Sound Production and Reception by Various Organisms. Dr. Pye theorized that all of the variations in the sound pulses of individual bat species represent a continuum. They may be derived from a single basic pattern

and the mechanisms which generate them have much in common. He presented a general theory which suggests that laryngeal or glottal sound pulses in all bats are nonsinusoidal and contain a number of harmonic components although the spectrum may vary in different species. Before emerging to the outside world these pulses are influenced by the acoustic properties of the air-filled cavities of the vocal tracts. According to the theory, these passive resonances alter both the relative phase and amplitudes of the sound components and lead to rapid changes of the phase and amplitude during frequency sweeps.

The anatomy of the dolphin vocal tract came under scrutiny by Dr. Purves. Past investigations have suggested that the various chambers, which are found in the upper part of the blow-hole, may be the sound source. By locating a sound source in the laryngeal tissue of dead dolphins and measuring the sound intensity at various points on the surface of the head, Dr. Purves showed that the greatest energy was distributed along the central axis of the skull, particularly at the tip of the snout. Since these measurements confirmed similar measurements which he made of the sound distribution emitted by living dolphins, he suggested that this is the mechanism of pulse beaming.

Measurements of phonation which use dead animals are subject to criticism in that the tissues have changed

in death. In order to circumvent this possibility, Dr. McKay suggested that the vocal mechanisms of living dolphins could be observed by the use of pulsed ultrasonic energy.

The site of sound reception by dolphins has also been a vexing question. Toward its answer Dr. Norris presented evidence which suggests that an area along each side of the lower jaw is the approximate site of sound reception. The tissue in question is unique in that it contains a large sack of oil. In support of this observation is the report of Dr. Grinnell that evoked potentials in the inferior colliculi of dolphins attained their maximum amplitude when a sound source was applied to the skin at this same location on either side of the lower jaw. Application of the sound source to other head regions, including the orifice of the external auditory meatus and melon, resulted in evoked potentials of lesser amplitude.

Engineering Models of Sonar Systems and Their Analysis.

The interest of the engineer in animal sonar systems is not so much from the standpoint of understanding the animal's behavior, as it is for the information that he can obtain from the animal system for application to man-made radar and sonar systems.

Dr. Griffiths discussed the characteristics of acoustic images and pointed out differences between these and optical images. Acoustic images comprise the specular reflections--the highlights of the object--whereas the light images also

contain a substantial contribution of light scattered by the surface of the object. In addition, he considered the measurement of spatial resolution which can be derived from the sound pulses of bats in terms of both the beam and frequency band widths. This led to a consideration of ambiguity functions which give an estimate of the maximum capabilities of an echolocating system when beam width, frequency band width and signal duration of the emissions are known. In sonar and radar systems, ambiguity functions depend upon the signal frequency and the signal length. In the man-made systems, there is a "trade-off" between range resolution and Doppler resolution. Dr. Cahlander continued the discussion of ambiguity diagrams by applying the concept to signals actually emitted by bats, Myotis l. lucifugus. For purposes of convenience, he classed the sounds emitted by this species of bats as the cruising, locating a target, pursuit and capture of the target signals. Ambiguity diagrams were generated by means of a computer to demonstrate the "trade-off" between pulse-length and pulse-duration in order to get range and relative velocity estimates of the target. For the particular pulse train that was analyzed, the cruising pulses were slightly more than ten times the duration and three times the amplitude of the pursuit pulses. According to the ambiguity diagram the cruising pulses represent a compromise between the maximum range and maximum velocity

resolution which these pulses can provide. As the bat approached the target, the target velocity information appeared to become less important than range information because the pulses became shorter. Both Drs. Cahlander and Griffiths pointed out that these estimates represent the maximum capability of the signals based on their physical characteristics. They do not necessarily mean that the animal can make the maximum use of the information which is available to it.

Range and relative target velocity information is, of course, vital to successfully intercept a target but other kinds of information are also necessary. Application of the engineering model has not yet been extended to the matter of azimuth and elevation of the target although several suggestions were made as to how this could be accomplished, e.g., wiggling the head back and forth to obtain several measurements of the interaural delay or by wiggling the ears back and forth at a high rate while emitting narrow frequency band signals, as the bats of one family (Rhinolophidae) are known to do. An additional observation was offered by Dr. Batteau for which no engineering model exists. This is the "cocktail hour effect"--the ability of an organism to direct its attention to one particular group of signals in a large conglomeration of signals.

Studies of Discrimination Capacities. Several papers,

which I would class as ecological, were presented concerning the discriminative capacities of bats and dolphins. Ecological, not in the sense that the animal was in its natural environment, but from the standpoint that the experimenter did not attempt to control the behavior of the animal during the measurement trials or the relevant characteristics of the stimuli--the sounds and their echoes.

Dr. Schnitzler reported that the smallest wires which Rhinolophidae were able to avoid were 0.08 mm in diameter. They frequently hit wires of smaller diameter. Dr. Möhres reviewed the data of echolocation acuity of three other families of Microchiroptera for which there is extensive information. The Vespertilionidea and Phyllostomatidae appear to be less able to detect fine wires than either the Rhinolophidae or Megadermatidae. The former two groups are able to detect and avoid wires of 0.12 - 0.157 mm diameter, whereas the latter two groups are able to detect and avoid wires of as little as 0.06 mm diameter.

Similar observations on the dolphin, Phocaena phocaena, were reported by Drs. Busnel and Dziedzic in tests of detection, by echolocation, of a metal wire, a nylon three-strand cord and a nylon monofilament. Metallic monofilaments were detected and avoided when they were of 0.05 mm diameter and larger, while the three-filament nylon cord was successfully detected when its diameter was 1 mm or larger. The nylon monofilament seemed to be the most difficult to detect.

A diameter of approximately 2 mm was required in order for the dolphin to achieve 90% avoidance. Furthermore, it made little difference in the results if the dolphin was permitted to utilize both echolocation and vision or if it was restricted to echolocation alone in the detection of these obstacles.

Several interesting points were raised by Dr. Griffin in his presentation of recent work in his laboratory. They related to the way in which bats distinguish between inedible and edible targets. Bats (Myotis l. lucifugus) were trained to catch meal worms which were shot from a "meal worm mortar". When the mortar charge of meal worms was mixed with small inedible objects, the bats caught almost anything. It appeared as though they could merely locate a small object but that they could not tell from the returning echo whether it was a meal worm, a piece of chalk, a marble, a rubber band, or small coin. After a number of days of training, it became apparent that the hungrier of the bats learned to reject the inedible objects. However, when spheres 3 - 8 mm in diameter were used, many days of practice were required before the bats consistently rejected 80 - 100% of the spheres while catching an equally large proportion of meal worms. It is not surprising that considerable practice was required in order for the animals to make this difficult discrimination since bats seldom find the air populated with small moving inedible pellets, in either natural or laboratory conditions, except when Dr. Webster's meal worm mortar is in operation.

A second important point is that the bats apparently made the discrimination between the edible and inedible objects when they were as far as 40 - 50 cm away from the targets. Dr. Griffin suggested that the decision to catch or reject was apparently made on the basis of echoes from the cruising type of pulses that sweep from about 100 to 40 Hz and which have a 2 msec pulse duration.

One factor which has been ignored in many of the experiments on detection of obstacles, wires, monofilaments, etc., is the role and possible confounding effects of spatial memory on this discrimination task. Dr. Neuweiler presented a series of observations in which the locations of wire squares were shifted from time to time. The results which he reported demonstrated that bats habitually prefer to pass through particular areas of the obstacle wire frame. When the wires were moved slightly in one direction or another, without changing the size of the apertures, a marked deterioration in avoiding the wires, by Rhinolophidae, resulted. Other evidence supports the preeminence of a spatial memory over echolocating signals in familiar surroundings. Dr. Möhres reported that when the roost cage was rotated by 90° after Rhinolophidae had left it on a feeding flight, they attempted to reenter the roost by the side of the cage from which they left. Eventually, they learned to enter the cage from the new position but if the cage is once more rotated, they continued to make errors in cage entry. They eventually

learned, however, to expect a different point of cage entrance after each trial and circled the cage until they found it. These data suggest that detailed spatial memories of the environment are constructed which are preeminent over echo-location information in familiar surroundings.

A second group of studies, which I tend to classify as behavioral, in contrast to those which I have called ecological observations, were conducted on the dolphin, sea lion, and man. They are distinguished from the ecological observations in that they are parametric studies of discrimination thresholds in which the experimenter has exercised control over the behavior of the animal and the stimulus conditions.

Dr. Norris reported measurements in which the dolphin, Tursiops truncatus, was taught to distinguish between a standard sphere of 6.35 cm diameter and a test sphere of 5.4 cm diameter. This was apparently a relatively easy discrimination in that performance was error free. When the test sphere diameter was increased to 5.71 cm, performance fell to approximately 77% success. However, when both spheres were 6.35 cm in diameter, the dolphin refused to participate in the experiment even though it had readily done so when the test sphere was smaller but apparently not discriminably so, as judged by lack of success in choosing the larger sphere.

One of the more amazing and interesting feats of which Tursiops seems to be capable is to select a 30 cm diameter, 0.21 cm thick aluminum disk when paired with other disks which are identical in all respects except thickness or material. Drs. Evans and Powell, in reporting these data, tend to favor an interpretation of the results which relies on a discrimination of reflected power of the echo from disks which differ in thickness or material, while Dr. McKay favors an interpretation which depends upon a discrimination of relative phase shift in the echo returning from the standard as compared to the variable target.

An exhaustive investigation of the use to which sounds are put by the California sea lion (Zalophus Californianus) was presented by Dr. Shusterman. In this series of well controlled studies, Dr. Shusterman demonstrated, quite clearly, that the California sea lion does not and cannot be trained to use the underwater sounds which it emits for the purpose of locating food. He did not, however, investigate the extent to which these underwater sounds may be used for spatial orientation.

The ability of humans to echolocate was the subject of three papers. Dr. Rice presented some well controlled psychophysical investigations of the abilities of blinded human subjects to detect targets of various diameters at various distances. When a hiss signal was used, the minimum acoustic angle for detection of a target was found to be 4.64° . In other experiments, the abilities of the observers

to detect edges and shapes of targets were tested.

Dr. Wilson reported results which indicated that echoes from sounds of broad band width take on a pitch which becomes higher as an obstacle is approached by a human observer. In addition to pitch itself, it is possible that rate of change of pitch may be important perimeter in the avoidance of obstacles. In order to investigate the phenomenon more closely, broad band sounds were generated and modified in several ways. When one of the interfering signals was phase inverted, a pitch was heard which could not be explained simply in terms of place or time analysis.

The phenomenon of "facial vision" was the subject of an investigation by Dr. Kohler. Facial vision is defined as a cutaneous sensation about the face and neck associated with the proximity of an obstacle. This sensation persists even though the skin of the face has been anesthetized by nerve block or the nerve supply to the face has been sectioned for the relief of intractable facial neuralgia. The results indicate that while the sensation is localized in the skin, it arises from another source--perhaps the ear.

Dr. Kay reported on the development of a device which makes use of microcircuitry for the emission of ultrasonic frequencies and detection of the resulting echoes. This device, according to Dr. Kay, has received enthusiastic user endorsement although a considerable amount of learning required in order to obtain maximum information concerning environmental obstructions. The sound transducers emit

broad band ultrasonic frequencies to take advantage of the superior obstacle detection capabilities inherent in them. The microphone pickups and electronic circuitry use the superheterodyne principle to translate the ultrasonic frequency echoes into sounds which are audible to the human ear. This tends to maximize object detection while allowing the subject to hear the returning echoes in a frequency range to which he is sensitive.

Social Communication Among Echolocators. The communicative character of the sounds emitted by Rhinolophidae was reported on by Dr. Möhres. When these bats have been maintained in captivity for some time, a definite roost-mate preference develops. It appeared that these bats emit signals which are unique for the individuals. In this way, a bat was able to signal its location to its preferred roost-mate. The nature of the "signature" is in some doubt. The pulses emitted by Rhinolophidae appear to be pure frequencies which change little except at the immediate onset and offset of the pulse. One possibility which has not been explored completely, is that each individual employs a unique frequency. Another aspect of social communication among bats concerns an "alarm reaction". There is apparently no special alarm call, although the flight reaction seems to be elicited by the perception of a special pattern of the orientation signals produced by Doppler shifts as the first bats hurriedly fly off. When recordings of such signals were made and played back to a group of resting horseshoe bats (Rhinolophidae), a considerable

disturbance and, in many instances, flight was induced.

Other evidence which supports the unique character of an individual bat's signal is found in the relationship of the mother to the young during the first flights of the latter. On its first flight, the young are guided by the mother. When the young lose connection with the mother during intervals of orientation sound emission by the mother, the young land at the next appropriate point and burst into rhythmical "distress" shrieks which attract the mother and cause her to reestablish acoustical guidance.

Social signalling in cetaceans must depend more heavily upon acoustic signals than for any other variety of mammal. According to the observations of Drs. Caldwell and Caldwell, the role of tactile signalling in both Inia geoffrensis and Tursiops truncatus also assumes major importance. Both species seem to derive pleasure from stroking any part of the body. Precopulatory behavior involves stroking by the flippers, sharp body contact, mouthing and nuzzling. The usual visual signs which impart a degree of social communication among other mammals, e.g., raising of hair, facial changes in primates and dogs, the laying back of ears, as well as threat signals made by the forepaws or arms, etc., are absent in dolphins. They are even denied the emotionally produced color changes so prominent in some cephalopods. Since it is generally agreed that the more social the species, the greater its need for complex social signals, the bottlenose dolphin and, to a lesser extent, Inia would

be expected to have a complex system of social sonar signals. In this regard, the whistle component of Tursiops' phonations undoubtedly carries a good share of the communication load. Each individual appears to have a characteristic whistle contour or "signature whistle." After birth of a bottlenose dolphin, the mother spends several days whistling and it was suggested that the infant learns the mother's characteristic whistle during this period. Variations in this signature whistle are also used when the bottlenose dolphin is in distress. A sharp explosive sound, a "crack", which is elicited from an adult under a fright situation, has also been identified. Sharp audible click sounds appear to be associated with exploratory situations and the complete absence of signalling could also be a communication signal, as when a new, unfamiliar object has been placed in a communal tank.

The report of Dr. Bastian is of particular interest to the comparative psychologist. It involved studies of communication between two dolphins in solving a lever pressing problem. A successful solution of the problem required cooperation and a transfer of information between the two animals. The task was simple. Two paddles were presented to each animal in its own enclosure. The paddle that was to be pressed by one animal on a particular trial was indicated by one of two alternative states of a light signal which was only shown to the other animal. Unless

this animal acted to transmit information about the state of the light to the paddle pressing animal, performance of the task would remain at a chance level. After suitable controls were instituted to insure that the animals were responding only to the information transferred by means of their own sounds, a sound barrier was imposed between them. At the imposition of the sound barrier the performance, which prior to its imposition had been at close to 100% correct, fell to a chance level.

Neurophysiological Investigations of Processing of Auditory Signals by Higher Nervous Centers of Echolocators. Only two investigations using the powerful tools of electrophysiology were formally reported at this conference. Both involved the central auditory system of bats. Informal discussions also included reference to the work of Dr. Suga (6) on the central nervous auditory system of bats.

Dr. Henson's results showed that the bat's acoustic system is specifically geared to protect and maintain its sensitivity during pulse emission. Prior to pulse emission, the middle ear muscles are activated. Contractions begin about 10 msec prior to pulse emission, attain a maximum contraction during pulse emission and relax during the FM sweep. Furthermore, the auditory units in the collicular nuclei recovered their sensitivity within 6 msec after the pulse, about twice as fast as that observed in anesthetized bats stimulated by artificial pulses and echoes. The

external ears appear to impart considerable directionality to the system in that the collicular evoked responses were maximum for a given sound intensity located directly ahead, as compared with those from the side or in back of the bat. These large differences appear to facilitate accurate sound localization. According to the electrophysiological results, the bat's ear is maximumly sensitive only during the interval between pulses. By controlling pulse repetition rate, bats appear to limit the echolocating depth of field and focus their attention on the particular target when many are potentially available.

Results of Dr. Grinnell's studies on neural units of the central auditory centers of bats showed that there is no reason to assume that echolocators have a superior temporal resolution of sounds arriving at the two ears as compared to nonecholocating animals. On the other hand, his results seemed to show that there is a unique feature, central enhancement of recovery, of these central units in echolocating animals that does not exist in nonecholocators. There appeared to be a recruitment of larger and larger populations of units in progressively more central nuclei to deal with "second-stimulus" (echoes or reverberations) information carried by only a very few of the primary auditory nerve fibers. Nonecholocators, on the other hand, appear to be organized in such a way that responses to echoes or reverberations are actively inhibited.

With respect to jamming signals, he reported that there is a binaural mechanism in bats which can selectively enhance the response to a signal in noise throughout the auditory system. For example, there is a reduced masking effect of noise in one colliculus when the signal is clearly detectable in the other. Noise has its expected masking effect at the level of the auditory nerve, but central to that the auditory system somehow comes to respond selectively to a signal that is largely masked at its input. In this way, the unusual resistance of bats to masking noises, even so loud that the echo signal is completely obscured, may account for the observation of Griffin, McCue, and Grinnell (2). Whether this particular binaural mechanism of selectively enhancing the central response to a signal is unique to echolocators, remains to be determined.

QUESTIONS RAISED

As is characteristic of good research, more questions have been raised by the results presented here than have been answered. Even a superficial listing of these questions would consume more space than is available. I shall confine my remarks to only a few of those which I find most interesting and for which it would be reasonably easy to devise experiments in order to obtain answers. One of the more interesting questions concerns the distribution of active echolocators among various species. According to Dr. Möhres, all members of the suborder of bats, Microchiroptera, possess

a more or less efficient sonar system. At the present time, however, of the Megachiroptera, only the Rousettus is known to use sonar, but only to a limited extent. One cannot help but wonder what the ecological determinants were which decreed that certain suborders would develop efficient sonar systems while only one genus of another suborder would have a comparable development. With respect to dolphins, only a few species have been demonstrated to echolocate actively. Are special structures or functional developments required for the effective use of echolocation in these animals as compared to others which do not apparently use this variety of information? Similarly, one wonders whether the other sense organs retain the high degree of sensitivity and acuity found in nonecholocators when the echolocators begin to depend more and more heavily upon this variety of spatial information.

Another group of questions arising from the results presented at this Symposium has to do with the auditory cues which the animal uses in interpreting information about its environment. To what extent, for example, does a shift in the phase of the echo, as compared to the emission, provide usable information to Drs. Evans and Powell's dolphins in making discriminations between aluminum plates of various thicknesses or between copper and aluminum plates of equal thickness? What is the least shift in sound frequency due to the Doppler effect, which the animal can detect and use

in target pursuit and capture? What are the limits of time discrimination, in both bats and dolphins, between emission and return of the echo? What are the limits of acuity of direction of the target and do the animals make use of these kinds of information?

Other questions have been raised concerning the structure and function of the sound emitting and sound detecting systems. One question is related to the rather peculiar anatomy of the auditory system of the dolphin in which the middle and inner ear, completely enclosed in bone, is separate from the rest of the skeleton of the animal. This has raised the question of whether the dolphin hears its own sound emission and if so, how does it protect the sensitivity of its hearing mechanism during emission so that it can be maximumly sensitive for the returning echo? In certain instances, dolphins appear to emit double clicks. If the second click is not an echo, it has been suggested that it may be some sort of compensatory mechanism to counteract oscillations in the mechanical parts of the auditory system due to the first click. How do dolphins make their variety of clicks, squeals, barks, grunts, and groans? Where is the vocal mechanism; how does it operate; is the emission beamed, and if so, how? An equally perplexing question arises when one tries to account for the site of receipt of the echo from the emitted sound. Certainly, some of the work presented at this Symposium suggests that the

external auditory meatus is not the avenue through which sounds travel to the middle and inner ears.

In certain species of bats, it is known that the signal frequently appears to overlap the time at which the echo should be returning. This raises the question of whether detection is possible when the sound emission overlaps the returning echo.

The answers to these questions are not easy to come by. While the fine and expensive sound recording and analyzing devices are of tremendous help in obtaining answers to these questions, the organism itself still remains the best detector and analyzer of its own signals. This was suggested early in the Symposium by Dr. Norris and certainly the research results presented here bear out his contention. While the statement is not apt to be challenged, the results reported here concerning the "signature" on signals of the Rhinolophidae to attract their preferred roost-mates, the "signature" whistle of the mother dolphin to its young, and vice versa, and evidence presented elsewhere that the killer whale is also capable of distinguishing between whistles of other killer whales strongly suggests that there are some components in these signals which our physical systems of sound analysis have not yet been able to detect or decipher. The selective attention, of which a listening organism is capable, but which is completely beyond the capabilities of a microphone and recording system, are best illustrated by

what Dr. Batteau has called the "cocktail party effect" and which I prefer to illustrate by the observation that a person listening to a symphony can follow the first violin part with little or no difficulty. All of these attest to the superior capabilities of the organism, compared to physical systems, at signal detection and analysis.

METHODS OF INVESTIGATION

I believe that the only method known at this time, which will give unequivocal answers to many of the questions, which I have mentioned and others which are inherent in the results reported by the participants of the Symposium, is one in which the organism, itself, is asked how it is making its discriminations. In this method, the animal must be taught to communicate with his human experimenter. In order to determine which cues are relevant and which are not useful to the animal, it is necessary for the experimenter to have absolute control of the experimental situation including, particularly, the stimulus situation. The techniques employed by Dr. Bastian, in investigating the communication capabilities of dolphins and Dr. Norris, in investigating the size discrimination capabilities of dolphins, would be particularly useful in extending investigations to the areas in which questions have been raised. Dr. Shusterman's work, demonstrating the absence of active echolocation for the detection of food targets, or Dr. Rice's measurements of echolocation acuity of humans may serve as models. Investigations of the frequency, intensity, phase and temporal discrimination characteristics,

using these techniques, would be particularly useful in assessing the probable cues which the animals use in detecting, avoiding, or pursuing targets.

Neurophysiological methods can tell us a great deal about how the nervous circuitry can accomplish the capabilities which the organism manifests in the behavioral studies. It can tell us little about what these capabilities are. These two methods, the behavioral and the electrophysiological, must work hand in hand in order to answer the questions of what is discriminated and how it is accomplished.

Applications of engineering principles and systems analysis to the echolocating systems of these animals can be very useful, particularly in regard to assessing the maximum information channel capacity of the organism. It is also quite likely that some useful applications to man-made sonar and radar systems can be derived from more intensive investigations of the animal systems. In this regard, the engineers and physicists are in an excellent position to improve and extend the biologists' and psychologists' information gathering capacity by providing them with more sophisticated instruments with which to accomplish the task.

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LE TRAITEMENT DE L'INFORMATION DANS LES SYSTÈMES BIOLOGIQUES

by
J. C. LEVY

Les systèmes biologiques donnent souvent l'impression, de mettre en défaut les lois de la physique classique. La sensibilité et la précision avec laquelle ils sont capables de détecter et de localiser des obstacles, semblent souvent un défi aux formules théoriques; en fait, il n'en est rien.

Cela tient aux faits suivants: Les systèmes nerveux, du moins, ceux des animaux supérieurs, peuvent accumuler des informations et les tenir en réserve. Il suffit alors parfois d'un imperceptible supplément d'information pour aboutir au résultat désiré.

L'exemple physique le plus simple que l'on puisse donner de ce phénomène, est celui de la réception d'un signal sinusoïdal pur de fréquence mal connue, que l'on sait seulement se situer dans une bande de largeur Δf , par un récepteur de bande passante.

On sait alors que le seuil de sensibilité du récepteur exprimé en puissance du signal est alors:

$$W_0 = T B \Delta f$$

ou T est la température absolue et B la constante de BOLTZMANN.

Mieux nous connaissons à l'avance la fréquence du signal, plus faible sera le niveau auquel nous pourrions le détecter.

En ce qui concerne la fréquence, il ne s'agit que d'une dimension, or un signal quelconque est défini par un très grand nombre de dimensions, cela se représente dans un espace fonctionnel tel que l'espace de HILBERT.

Pour donner du principe une représentation imagée, nous nous contenterons de représenter cet espace avec deux dimensions, qui situeront pour chaque signal, un point dans un bassin rempli d'eau trouble dont la profondeur représente le seuil de sensibilité du système.

Les deux dimensions du fond du bassin correspondent à sa définition, en durée, spectre de fréquence, forme géométrique ... etc

La hauteur correspond à son intensité, ou plus exactement au logarithme de son intensité.

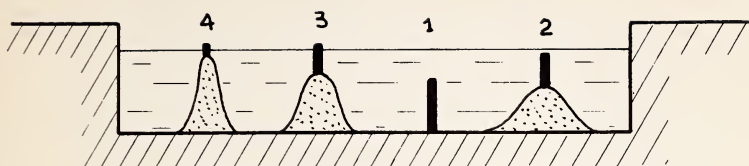
Ceci dit, chaque signal correspond à un objet d'une hauteur donnée, déposé en un point donné du bassin. Si l'objet émerge, il est détecté, s'il reste immergé, il n'est pas détecté, mais n'est pas forcément perdu.

Si plusieurs objets sont immergés au même endroit, leur accumulation peut permettre à un dernier objet d'émerger, eut-il une hauteur très inférieure à celle du bassin.

Il est inutile d'essayer de combler le bassin car on ferait remonter le niveau de sa surface, dans une telle représentation, cela exprime la faculté du système nerveux de ne laisser sortir qu'un certain nombre de signaux. Un signal bien caractérisé, correspond ici à un tas haut et étroit qui affleure à la surface. Il suffit d'y rajouter un élément de faible hauteur pour faire émerger le signal. La position du point d'émergence fournit alors l'information désirée.

La figure 3 donne une idée de ce principe.

Fig. 3



Le signal 1, bien que le plus intense, n'est pas perçu, de même que le signal 2, alors que les signaux 3 et 4 le sont.

Les exemples biologiques de ce principe sont extrêmement nombreux, tant chez l'homme que chez l'animal; bornons-nous à quelques exemples classiques.

- Chez l'homme : Le sommeil "de nourrice" au cours duquel la nourrice ne peut être réveillée que par la voix de l'enfant dont elle a la garde. La possibilité de suivre une conversation dans un bruit ambiant plus intense.

- Chez l'animal : Les meilleurs exemples sont donnés par les systèmes SONARS, capable de détecter des obstacles de faibles dimensions, chaque animal pouvant identifier l'écho de sa propre voix dans un bruit ambiant plus intense.

Les systèmes biologiques supérieurs possèdent, grâce à leurs milliards de cellules nerveuses, la possibilité de caractériser un signal par un nombre de paramètres infiniment supérieur au seul paramètre "fréquence" utilisé par nos récepteurs radio classiques.

La quantité d'information accumulée au préalable est alors énorme. Il en résulte que pour des signaux répondant à certaines caractéristiques bien définies, de tels systèmes peuvent constituer des récepteurs doués d'une sensibilité et d'une précision que ne saurait atteindre aucun dispositif de fabrication humaine.

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